



RECORDS OF THE AUSTRALIAN MUSEUM



Volume 35 Contents

RECORDS OF THE AUSTRALIAN MUSEUM

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Revision of the Genus *Micronereis* (Polychaeta: Nereididae: Notophycinae)

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ABSTRACT. The genus *Quadricirra* Banse, 1977 is not recognized, since its principal diagnostic character, the presence of accessory parapodial cirri, is sexually dimorphic and cannot be correlated with other characters; thus *Micronereis* is the sole genus of the subfamily Notophycinae. A new species, *M. piccola*, is described and *M. siciliensis* and *M. bodegae* are synonymized with *M. variegata* and *M. nanaimoensis* respectively. A key to males and descriptions of all species are provided. The Notophycinae appears to be the most derived subfamily of Nereididae, characterized by a combination of epitokal modifications retained from their nereidid relatives and specializations acquired as members of the meiofauna.

PAXTON, H., 1983. Revision of the genus *Micronereis* (Polychaeta: Nereididae: Notophycinae). Records of the Australian Museum 35(1):1-18.

The polychaete family Nereididae is divided into four subfamilies (Banse, 1977a, b): the Nereidinae, Namanereidinae, Gymnonereidinae and Notophycinae. Banse (1977a) recognized the latter subfamily, originally proposed as Notophycidae by Knox and Cameron (1970) for *Notophycus* only, to include the genera *Micronereis* (and its synonyms *Notophycus* and *Phyllodocella*) and *Quadricirra*. *Quadricirra* Banse, 1977 was erected for *M. halei* Hartman, 1954 from South Australia and an indeterminate species from the Suez Canal that had been reported as an aberrant specimen of *M. variegata* by Fauvel (1927). *Quadricirra* was distinguished from *Micronereis* by the presence of accessory cirri on the lower notopodia and upper neuropodia in the former genus and their absence in the latter. A new species from north-west Australia was described as *Q. bansei* by Hartmann-Schröder (1979). The latter author recognized that the accessory cirri were present only in the males of *Q. bansei* and amended the genus accordingly.

While identifying specimens of Notophycinae I realized that the presence of accessory parapodial cirri is a male epitokal modification. Epitoky is characteristic of the Nereididae; most species metamorphose and swarm for breeding (Clark, 1961). Epitoky in species of Notophycinae has been overlooked, since the changes are relatively minor compared to some other nereidids. However, as Clark (1961:200) pointed out: "The structural modifications associated with epitoky may be no more than an elongation of the chaetae, or it may involve the wholesale reconstruction of the musculature and modification of the sense organs as well as the

enlargement of the parapodia and replacement of the chaetae."

Although notophycines have a wide geographical distribution (Fig. 1), not many specimens have been reported. All known species are small (up to 15 mm) with relatively few segments (up to 26), and are thus members of the meiofauna. The rarity of their collection is attributed to their small size and preferred habitat. Most specimens have been collected in the littoral zone or in lagoons in depths from 0 to 3 m, sometimes by scuba divers with hand-held corers. The deepest record is that of a specimen of *M. eniwetokensis* which was collected from a depth of 30 m (Reish, 1961). The worms are generally associated with algae, which appear to be their main food source.

The morphology and taxonomy of the Notophycinae have been unclear. The aim of this paper is to examine and describe the characteristics of the notophycines in order to distinguish features held in common with other nereidid subfamilies from those that arose as meiofaunal adaptations, and to review their taxonomy and to provide descriptions for all known species.

Materials and Methods

The material examined was loaned by and/or is deposited in the following institutions: Allan Hancock Foundation, University of Southern California, Los Angeles (AHF); Australian Museum, Sydney (AMS); British Museum (Natural History), London (BM); CSIRO Division of Fisheries and Oceanography, Cronulla (CSIRO); Canterbury Museum, Christchurch

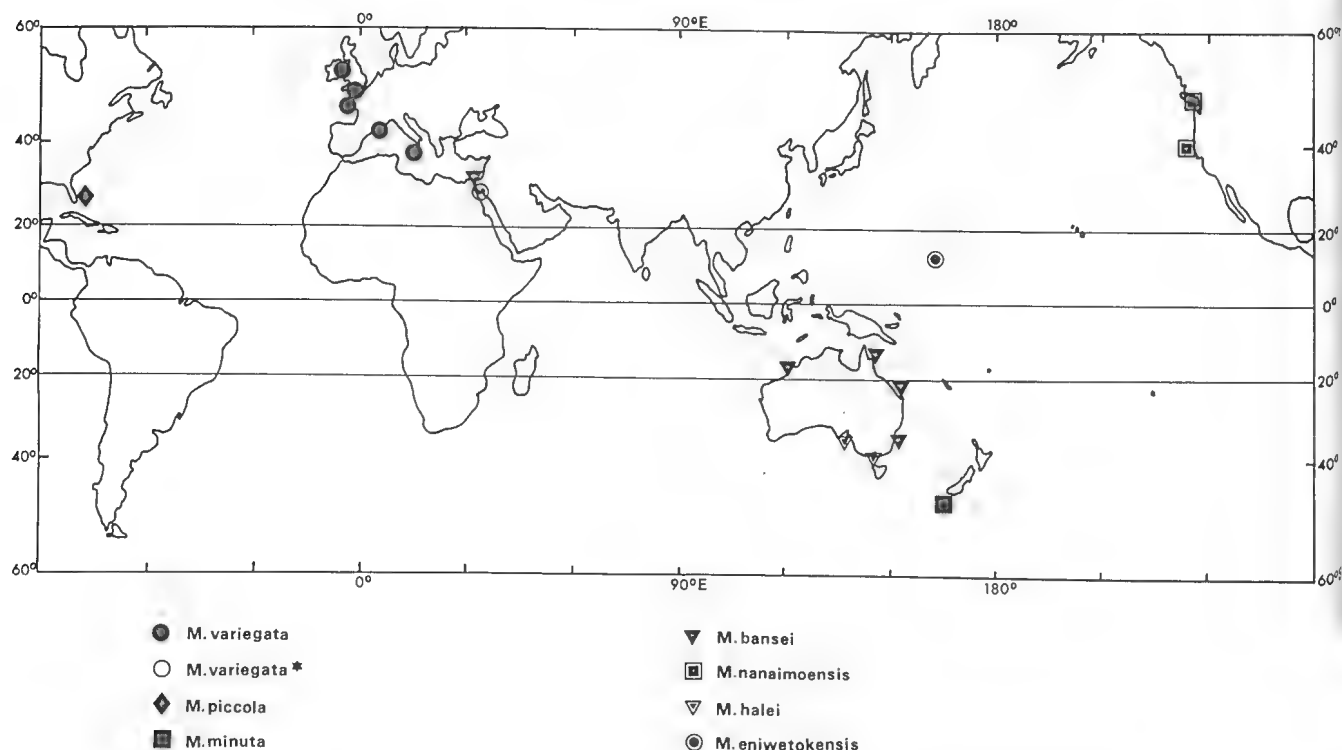


Fig. 1. Geographic distributions of *Micronereis* spp. *Reported as *M. variegata*, but possibly *M. bansei* (see text).

(CM); Istituto Policattedra di Biologia Animale dell' Università di Catania (IPC); National Museum of Victoria, Melbourne (NMV); University of Canterbury, Zoology Department, Christchurch (UC); Smithsonian Institution, Washington (USNM); Western Australian Museum, Perth (WAM).

The specimens were examined with a stereoscopic dissecting microscope or temporarily mounted in 50% (v/v) glycerine and examined with a compound microscope. To examine the jaw apparatus, it was often necessary to make a dorsal incision and dissect out the complete pharynx and buccal tube, which were later permanently mounted. All drawings were prepared with the aid of a camera lucida.

The references listed are extensive but not complete; only those providing new records or information are included.

GENERAL CHARACTERS

The general characters of Notophycinae and information on their life histories are discussed below and compared in Table 1.

General Morphology of Atokes

Prostomium. The prostomium (Figs 3, 14) is round to subquadrate, sometimes weakly bilobed, and about as long as wide. It bears two pairs of eyes; the anterior pair is larger than the posterior pair and has more obvious lenses. The prostomium lacks antennae but bears at the anterior margin a pair of ventrally directed,

rounded protrusions (Figs 15, 28). These structures have been referred to as palps (Berkeley and Berkeley, 1953; Hartman, 1954; Reish, 1961; Cantone, 1971; Hartmann-Schröder, 1979), as upper lips (Rullier, 1954), as frontal lobes (Fauchald and Belman, 1972), and as epidermal lobes (Banse, 1977a). These protrusions were observed as ciliated organs in six-setiger larvae of *Micronereis variegata* (Rullier, 1954), and are similar to the development of the palps of *Nereis diversicolor*, belonging to the nominate subfamily, which begin to develop in four-setiger larvae (Dales, 1950). I therefore follow the majority of authors and term the structures palps. The paired palps are spherical to subconical, small to very small so that they are sometimes difficult to observe. The notophycine palps differ from those of other nereidids in occupying a more central position and lacking palpostyles. The lack of palpostyles, which only develop in *N. diversicolor* when the young worm consists of 18 setigers (Dales, 1950), is perhaps a neotenic character in notophycines, related to their small size.

Peristomium or tentacular segment. The peristomium is very short, forming a distinct apodous segment. It is usually not clearly visible, but may be seen dorsally as a narrow ring (Fig. 14); it is only distinct ventrally when the anterior buccal tube is everted (Fig. 16). There are four pairs of tentacular cirri inserted lateral to the prostomium (Fig. 3). The anterior two pairs, arising in front of the anterior pair of eyes, have been referred to as lateral antennae by some authors. The anterior two pairs of tentacular cirri are shorter than the posterior two pairs which arise from the

peristomium. The fourth pair may be greatly elongated in some species, such as *M. eniwetokensis* and *M. bansei*, where they reach setiger 4–5 in some specimens (Fig. 14). Rullier (1954) has shown that the four pairs of tentacular cirri in *Micronereis variegata* are homologous to those of other nereidids and develop in the same way.

Proboscis. In contrast to those of other nereidids, the notophycine proboscis is not fully eversible. Yet its morphology and armature are closer to the typical nereidid proboscis than has generally been accepted (Fig. 16); terminology follows Dales (1962). The muscular pharynx lies within the anterior three to five segments and contains a pair of jaws. The buccal tube lies between the pharynx and the mouth and like the typical nereidid buccal tube, contains denticles or paragnaths. However, the notophycine buccal tube differs markedly in that it cannot be turned completely inside out: only the anterior part can be protruded. Although the pharyngeal jaws are movable, the pharynx cannot be everted.

The paired jaws are of two types: (1) bulbous proximal area with a distal apex and three to five teeth on the cutting edge of the distal half (Figs 16, 18); or (2) greatly reduced proximal area with a prolongation beyond the distal apex (Fig. 12). The former shortened type of jaw is found in all adult females and in males of four species, while the latter prolonged type of jaw is found in males of the remaining four species (Table 1).

The notophycine paragnaths are very lightly sclerotized and thus difficult to observe; they have not been seen in some species. The anterior part of the buccal tube may contain numerous paragnaths, arranged in regular rows (Fig. 16), which develop from simple cones in juveniles into crown-shaped structures with four to eight cusps in adults (Figs 4, 17). The number of cusps on the crown is of limited taxonomic value (Table 1). The numerous crown-shaped oral paragnaths are reminiscent of mollusc radulae. However, Rullier (1954) has pointed out that their function is different. He found that the gut contents of *M. variegata* were irregular fragments of algae rather than a ground-up pulp and suggested that the oral paragnaths catch and retain algal fragments which are then torn up by the jaws.

The posterior part of the buccal tube contains two to six paragnaths. The most constant of these are the median paragnaths which are found at the junction of the buccal tube and the pharynx and consist of two light yellow bars with two darker, irregularly shaped denticles (Fig. 16). The orientation of the bars changes with pharyngeal movement, so that the bars may lie in a straight line and appear as one (Figs 16, 34), or they may form a V-shape (Fig. 5). Rullier (1954) described up to four additional accessory paragnaths for *M. variegata*; they were associated with the median one but were irregular in shape and varied in number. They have not been observed in any of the other species.

Since the paragnaths of the anterior part of the buccal tube of notophycines correspond to those of the oral ring of typical nereidids and the paragnaths of the

posterior part of the buccal tube correspond to those of the maxillary ring, it is proposed that the conventional nereidid terminology be applied and the crown-shaped paragnaths be referred to as oral, and the median and accessory paragnaths as maxillary paragnaths.

Parapodia. The first two setigerous segments are short and their parapodia are uniramous; the neuropodia have long setal lobes with ventral cirri; dorsal cirri are lacking. The first pair of parapodia is directed strongly anteriorly and ventrally, and the second pair to a lesser degree. The following parapodia are biramous, with notopodia and neuropodia widely separated and directed laterally (Fig. 6). The parapodia are often ciliated (Fig. 22), and have dorsal and ventral cirri, but no ligules. Structures referred to by previous authors as ligules or digitate lobes are considered to be sexually dimorphic accessory cirri (see below).

Each of the parapodial rami is supported by a single yellow aciculum. The setae diverge from the aciculum in fan-shaped bundles. Those of the anterior uniramous setigers are shorter and finer than those of the following ones. The setae are spinigers (Fig. 8); the articulation is generally homogomph but approaches in some cases the hemigomph condition. The shaft of a seta is transparent and the core may have distinct, weak, or no septa. The distal end of the shaft is crenulated, ranging from distinct (Fig. 29) to barely visible. The blades of *M. minuta* are coarsely serrated while those of all other known species are finely serrated. The structure of the serrations is best seen in *M. nanaimoensis* (Fig. 29); each serration ends in a hair-like extension that is twice as long as the serration. The extensions may be present in all species with finely serrated blades but are not always clearly visible.

Segmental eyespots. Small pigment spots on the posterolateral corners of each segment from setiger 4 onwards were observed in some individuals of four species (Table 1). The pigment spots resemble the eye in shade and density and are interpreted as segmental eyespots. The degree of pigmentation differs, so that for a given species the eyespots range from absent to well-developed. They were observed in some males, females and juveniles and cannot be correlated with sex or maturity.

Pygidium. The pygidium is a small lobe with a dorsal anus and a pair of anal cirri.

Sexual Dimorphism and Epitokal Modifications

Modifications common to both sexes. Enlarged eyes are found in both males and females of *M. bansei*; in the females, the enlargement causes the fusion of the anterior and posterior eyes, yet they remain in a dorsal position (Fig. 14); in the males the enlargement proceeds so far that the anterior eyes take up a ventral position (Fig. 15).

Modifications in males. The males of five species (Table 1) have copulatory hooks on the neuropodia of setiger 3 which aid in holding on to the female during

Table 1. Comparison of species of *Micronereis*

Species	<i>M. variegata</i>	<i>M. piccola</i>	<i>M. minuta</i>
Length (mm)	♂ ♂ 2-4 ♀ ♀ 4-8	♂ 1.7 ♀ 2.0*	♂ 3.6 ♀ ♀ up to 5.8
Setigers (number)	♂ ♂ 16-21 ♀ ♀ 21-23	♂ 15 ♀ 16*	♂ 22 ♀ ♀ 24
Oral paragnaths	present	present	present
Number of cusps on crown	4	4	?
Maxillary paragnaths	present	present	present
Median	2 bars	2 bars	2 bars
Accessory	up to 4	not observed	not observed
Segmental eyespots	not observed	present	not observed
Spiniger			
Shaft	no septa	faint septa	no septa
Blade	finely serrated	finely serrated	coarsely serrated
Male characteristics			
Jaws (type)	prolonged	prolonged	prolonged
Accessory parapodial cirri	absent	absent	present
Copulatory hooks on setiger 3	present	present	absent
Number	2	2-3	—
Ornamentation of hook	5-7 spines	4-6 spines	—
Simple setae	absent	absent	present
Other type of setae	absent	falcigers	absent
Female characteristics			
Mucous egg cocoon	present	†	†
Diameter of cocoon (mm)	3-5	†	†
Number of eggs per cocoon	20-80	†	†
Diameter of egg (µm)	240-350	†	†
Colour of eggs	red	†	†
Distribution (Fig. 1)	France; England; Italy; ? Sinai Peninsula	Bahamas	Snares Island, New Zealand

*not fully grown †unknown

coupling. *M. nanaimoensis* has the most elaborate hooks, which have a crest with several spines (Fig. 30), while the hooks of the other four species are distally more or less recurved and bear several spines but no crest (Fig. 9).

Parapodial appendages (Fig. 11) are found on the lower side of the notopodia and the upper side of the neuropodia in males of four species (Table 1). These appendages were regarded as ligules by Fauvel (1927), as cirri by Gravier (1934), as digitate lobes by Hartman (1954) and as accessory cirri by Banse (1977a). Parapodial ligules are typical for members of the nominate subfamily; they are coelomic extensions of the parapodial rami. In contrast, the notophycine structures are attached appendages that can easily separate (Fig. 20). The appendages are thin-walled with a well-developed capillary network; they constitute branchiae or cirri and are referred to herein as accessory cirri. They are absent in young atokous males of *M. halei* and develop at the onset of epitoky.

The males of most species of *Micronereis* undergo some setal changes associated with maturity (Table 1). In its simplest form, the change consists of the addition of slender simple setae, as in *M. nanaimoensis* and *M. minuta*. The change in the setal pattern may involve the transformation of spinigers to compound falcigers, as in *M. halei* (Fig. 32). Partly transformed males possessed some spinigers in which the blades had very fine distal tips which were often bent (Fig. 33). These spinigers become progressively replaced or changed into falcigers. *M. bansei* is the only known species in which spinigers are replaced by simple setae (Fig. 27) and falcigers (Fig. 26).

Modifications in females. Mature females are generally larger than males and consist of a greater number of setigers. The parapodial lobes are enlarged and inflated and have a bulbous area or papilla at the base of the dorsal cirrus (Fig. 23); this presumably serves as a gonopore for the passage of eggs. The dorsal cirri of the median to posterior dorsal cirri may enlarge and

<i>bansei</i>	<i>M. nanaimoensis</i>	<i>M. halei</i>	<i>M. eniwetokensis</i>
up to 2.1 up to 3.8	♂ ♂ up to 13 ♀ ♀ up to 15	♂ ♂ up to 6.7 ♀ †	♂ 1.7* ♀ 1.8*
20 22	♂ ♂ 23 ♀ ♀ 26	♂ ♂ 27 ♀ †	♂ 14* ♂ 18*
ent	present	not observed	not observed
ent	5	—	—
rs	not observed	not observed	present
observed	—	—	2 bars
ent	not observed	not observed	not observed
ent	not observed	present	present
septa y serrated	distinct septa serrated	no septa finely serrated	faint septa finely serrated
ened ent ent	shortened absent present	shortened present absent	shortened absent absent
spines ent gers	5 or more crested present absent	— — absent falcigers	— — absent absent
ent 1.6 190	present 10–20 many hundreds 200 green	† † † † †	† † † † †
ern Australia, Queensland South Wales, Australia; Said, Egypt	British Columbia, Canada; Washington, California, U.S.A.	South Australia, Victoria Australia	Eniwetak Atoll, Marshall Islands

develop lamellar folds, as in *M. variegata* and *M. bansei* (Fig. 23), or may remain small throughout, as in *M. nanaimoensis*.

TAXONOMY

Family NEREIDIDAE Johnston, 1865

Subfamily NOTOPHYCINAE Knox and Cameron, 1970

Type-genus: *Micronereis* Claparède, 1863.

Micronereis Claparède

Micronereis Claparède, 1863:57. Type-species: *M. variegata* Claparède, 1863, by monotypy. Gender: feminine.
Notophycus Knox and Cameron, 1970:75. Type-species: *N. minutus* Knox and Cameron, 1970, by monotypy and original designation. = *Micronereis minuta*.

Phyllodocella Fauchald and Belman, 1972:107. Type-species: *P. bodegae* Fauchald and Belman, 1972, by monotypy. = *Micronereis nanaimoensis* Berkeley and Berkeley, 1953.
Quadricirra Banse, 1977a:125. Type-species: *Micronereis halei* Hartman, 1954, by original designation.

Remarks: Both *Notophycus* Knox and Cameron and *Phyllodocella* Fauchald and Belman were referred to *Micronereis* by Banse (1977a). The principal diagnostic character of *Quadricirra*, the presence of accessory parapodial cirri, is found in epitokous males of four species (Table 1), but is absent in atokous males and females. Since this sexually dimorphic character cannot be correlated with other diagnostic characters, e.g. type of jaw and presence of copulatory hooks, it is not considered to be of generic significance. Thus *Quadricirra* is considered to be a junior synonym of *Micronereis*, leaving the latter as the sole genus of the subfamily Notophycinae. *Quadricirra halei* (Hartman, 1954) and *Q. bansei* Hartmann-Schröder, 1979 are referred to *Micronereis*. The specimen from the Suez

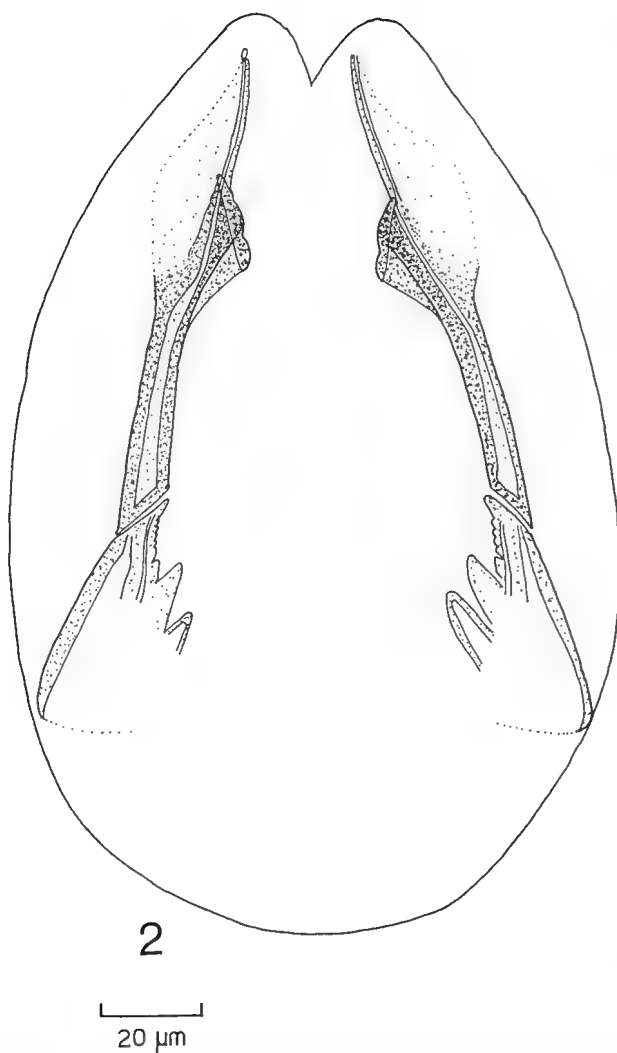


Fig. 2. *Micronereis variegata*, jaws of male (pressure of mounting caused fracture of distal prolongation). (Holotype of *M. siciliensis*, IPC).

Canal reported as *Quadricirra* sp. by Banse (1977a) was found to agree with *M. bansei*.

Micronereis variegata Claparède
Figs 1, 2

Micronereis variegata Claparède, 1863:57 pl. 11:figs 5-7, (Normandy, France); 1864:582, pl. 8:figs 4, 4a.—Quatrefages, 1865:578.—Saint-Joseph, 1888:268.—Racovitza, 1893:1390; 1894:153.—Caullery and Mesnil, 1898:—Fauvel, 1900:315; 1923:332, fig. 128a-f.—Elwes, 1909:350.—McIntosh, 1910:261, fig. 63, pl. 86:fig. 8.—Regnard, 1913:91, figs 3-11.—Herpin, 1925:119.—Rullier, 1954:195, figs 1-43.—Southward, 1956:263.—Reish, 1961:273.—Banse, 1977a:121.—Amoureux *et al.*, 1978:81.

Micronereis siciliensis Cantone, 1971:926, figs 4-9 (Catania, Sicily).—Banse, 1977a:121.

Material examined. *England*: Plymouth—1 ♂ and 1 ♀ (USNM 35680). *Sicily*: Catania, Cannizzaro—♂ HOLOTYPE and ALLOTYPE of *M. siciliensis* (IPC).

Diagnosis. Jaws of males of prolonged type, shortened in adult females. Accessory parapodial cirri absent. Spinous copulatory hooks present in males. Homogomph spinigers; shafts without septa; blades finely serrated.

Description. Length of males 2–4 mm (16–21 setigers), females 4–8 mm (21–23 setigers). Prostomium rounded with pair of ventral palps and 2 pairs of eyes with lenses. Four pairs of short, subulate tentacular cirri. Oral paragnaths crown-shaped with 4 cusps (Rullier, 1954, fig. 13); up to 6 irregularly shaped maxillary paragnaths, of which median ones are most constant (Rullier, 1954, figs 10, 12). Pair of sexually dimorphic jaws (see below). Biramous parapodia sometimes ciliated, with subulate dorsal and ventral cirri; homogomph spinigers: shafts without septa, blades finely serrated. Pygidium with pair of anal cirri.

Male characteristics. Jaws with 3–4 proximal teeth and distal prolongation (Fig. 2). Setiger 3 with 2 neuropodial copulatory hooks each with 5–7 spines. No obvious epitokal changes.

Female characteristics. Jaws of juveniles of prolonged type, jaws of adult females with shortened type with 3–4 teeth.

Biology. Rullier (1954) gave a detailed account of the reproduction and development of *M. variegata*.

Remarks. It was not possible to locate the holotype of *M. variegata* or to obtain specimens from the type locality. However, the specimens from Plymouth agree well with the original description and presumably they are identical.

Cantone (1971) described *M. siciliensis* from Catania, Sicily. She stated that it differed from *M. variegata* in (1) the shape of the male jaw, (2) the presence of palps in the female only, and (3) the copulatory hooks being more recurved. She also mentioned that a capillary seta was found in the posterior segments. Examination of the type material of *M. siciliensis* showed the following: (1) The jaws of the male holotype were figured upside down and misinterpreted by Cantone (1971, fig. 9). The pressure of the slide has fractured the distal prolongation at the point where it breaks off in females, so that the jaw appears to consist of different pieces. When the jaws are viewed in their proper orientation and the weakly sclerotized detail is observed, they are characteristic of *M. variegata* (Fig. 2). (2) Although the palps are more prominent in the female allotype, they are also present in the male holotype. (3) The holotype has only one uniramous segment, while the allotype has the usual two. This condition is considered to be a case of abnormal development. The copulatory hooks are present on the first biramous segment, which in this case is setiger 2 instead of 3. The distal part of the copulatory hook is recurved normally and has about 5 spines, which is within the range of *M. variegata*. No capillary setae were found in the posterior setigers of the complete holotype; the allotype is incomplete.

Banse (1977a) considered the low number of segments, “especially in the male”, as another

distinguishing feature of *M. siciliensis*. The holotype consists of 15 setigers but it lacks setiger 1, so that a normal male would have at least 16 setigers, while the two females were incomplete and the number of setigers is not known. The Mediterranean population of *M. variegata* was reported by Racovitza (1893) as attaining 16–17 setigers in the males.

Based on these observations, it is concluded that the specimens described as *M. siciliensis* agree with *M. variegata* and the former name is considered as a junior synonym of the latter.

Amoureux *et al.*, (1978) reported *M. variegata* from the Sinai Peninsula. The authors stated that the specimens had shortened jaws and lacked accessory parapodial cirri. Unfortunately, the specimens could not be examined during the present study. Since *M. bansei* occurs at Port Said, it is possible that the specimens from the Sinai Peninsula are females of *M. bansei* rather than *M. variegata*.

Distribution: France, England, Italy and questionably Sinai Peninsula (Fig. 1).

Micronereis piccola n. sp.

Figs 1, 3–10

Material examined. *Bahamas*: Cherokee Sound, Abaco, c. 26°N, 77°W, from submerged plastic sponges, Spring 1972, A. Schoener, collector—♂ HOLOTYPE (USNM 54514) and 1 ♂ and 4 ♀ PARATYPES (USNM 60505–8); *Bimini*, south portion of Bimini Lagoon, c. 25°43'N, 79°16'W, March and April 1970 and January 1971, A. Schoener, collector—1 ♂ and 3 ♀ PARATYPES (USNM 60509–10) and 2 additional specimens (USNM 60511).

Diagnosis. Jaws of males of prolonged type, proximal teeth absent; shortened type in adult females. Accessory parapodial cirri absent. Extended notopodial lobes above dorsal cirrus with several setae. Spinous copulatory hooks present in males. Compound homogomph spinigers with weak septa in shafts; finely serrated blades in females and atokous males; spinigers and falcigers in epitokous males.

Description. Length of male holotype 1.7 mm for 15 setigers; width 0.25 mm without and 0.60 mm with parapodia. Length of young male paratype 1.0 mm for 12 setigers and of female paratypes 0.95–2.0 mm for 14–16 setigers.

Prostomium rounded with pair of small ventral palps and 2 pairs of eyes with lenses, anterior pair larger than posterior pair (Fig. 3). Four pairs of cirriform tentacular cirri; 2 anterior pairs shortest, about 1.5 times length of prostomium, 3rd pair twice length of prostomium, 4th and most posterior pair longest, reaching setiger 4–5. Oral paragnaths crown-shaped with 4 cusps (Fig. 4), maxillary paragnaths 2 light bars (Fig. 5), pair of sexually dimorphic jaws (see below). Biramous parapodia with notopodia and neuropodia each with single aciculum; sparse ciliation observed in young paratypes; notopodia with bulbous extensions above dorsal cirri; long, cirriform dorsal and ventral cirri (Figs 6, 7). Each fascicle with about 10 homogomph spinigers,

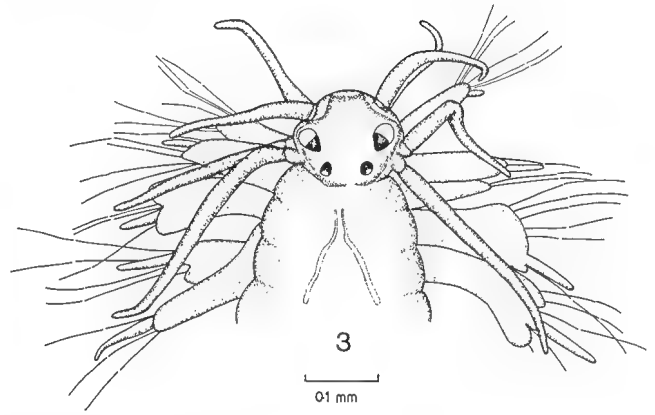


Fig. 3. *Micronereis piccola*, n.sp., anterior end of male, dorsal view. (Holotype, USNM 54514).



Fig. 4. *Micronereis piccola*, n.sp., jaw and oral paragnaths of adult female. (Paratype 1, USNM 60505).

superior 2–3 projecting above dorsal cirrus; shafts with weak septa (visible with 1000× magnification), blades finely serrated (Fig. 8). Segmental eyespots in some

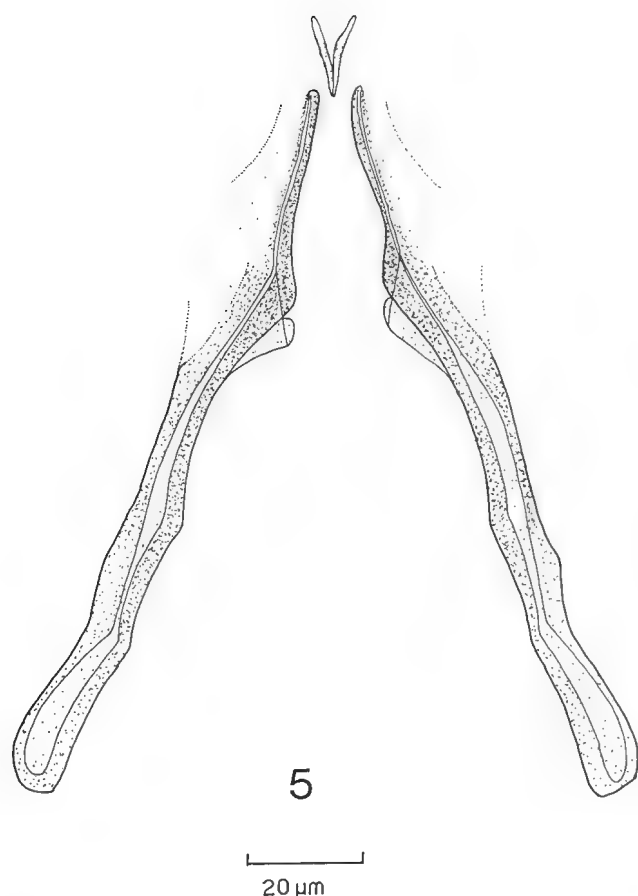


Fig. 5. *Micronereis piccola*, n.sp., jaws and maxillary paragnaths of adult male. (Holotype, USNM 54514).

specimens from setiger 4 onwards. Pygidium with pair of long cirriform anal cirri.

Male characteristics. Jaws of prolonged type, proximal teeth absent (Fig. 5). Setiger 3 with 2–3 neuropodial copulatory hooks, each with 4–6 spines (Fig. 9). Accessory parapodial cirri absent. Spinigers transformed into falcigers during epitoky (Fig. 10).

Female characteristics. Jaws of juveniles with distal prolongation and proximal teeth; adult females with shortened jaws with 3 teeth (Fig. 4).

Biology. The male holotype contained sperm morulae and free spermatozoa. Epitoky was in an early stage, as parapodia 6 and 7 had few falcigers; a less mature male paratype had only compound spinigers. The female paratypes were immature.

Remarks. The presence of prolonged jaws and copulatory hooks in the males links *M. piccola* to *M. variegata*. *M. piccola* differs in having jaws of the males lacking proximal teeth, and in having longer tentacular, dorsal and ventral cirri, more extended lobes above the

dorsal cirri with several notopodial setae, and septa in the shafts of the compound setae.

The name *M. piccola* refers to the small size of this species.

Distribution. Bahamas (Fig. 1).

Micronereis minuta (Knox and Cameron)

Figs 1, 11–13

Notophycus minutus Knox and Cameron, 1970:75, figs 1–5 (Snares Island, New Zealand).

Micronereis minuta.—Banse, 1977a:123, pl. 1:figs e–i.

Material examined. New Zealand, Snares Island, Boat Harbour, from red algal washings in *Durvillea* zone, intertidal, 15 January 1967—HOLOTYPE and 2 PARATYPES (CM AQ 3466); Snares Island, Boat Harbour, Senecio Pool, on red algae, 0–2 m, 20 January 1975, C.E. Holmes, collector—1 ♂, 8 ♀♀, 5 juveniles (CM AQ 3505).

Diagnosis. Tentacular cirri with thin terminal article. Jaws of males of prolonged type, shortened type in females. Accessory parapodial cirri present in epitokous male, absent in females. Copulatory hooks absent. Homogomph spinigers lack septa in shafts, blades coarsely serrated; additional capillary simple setae in epitokous male.

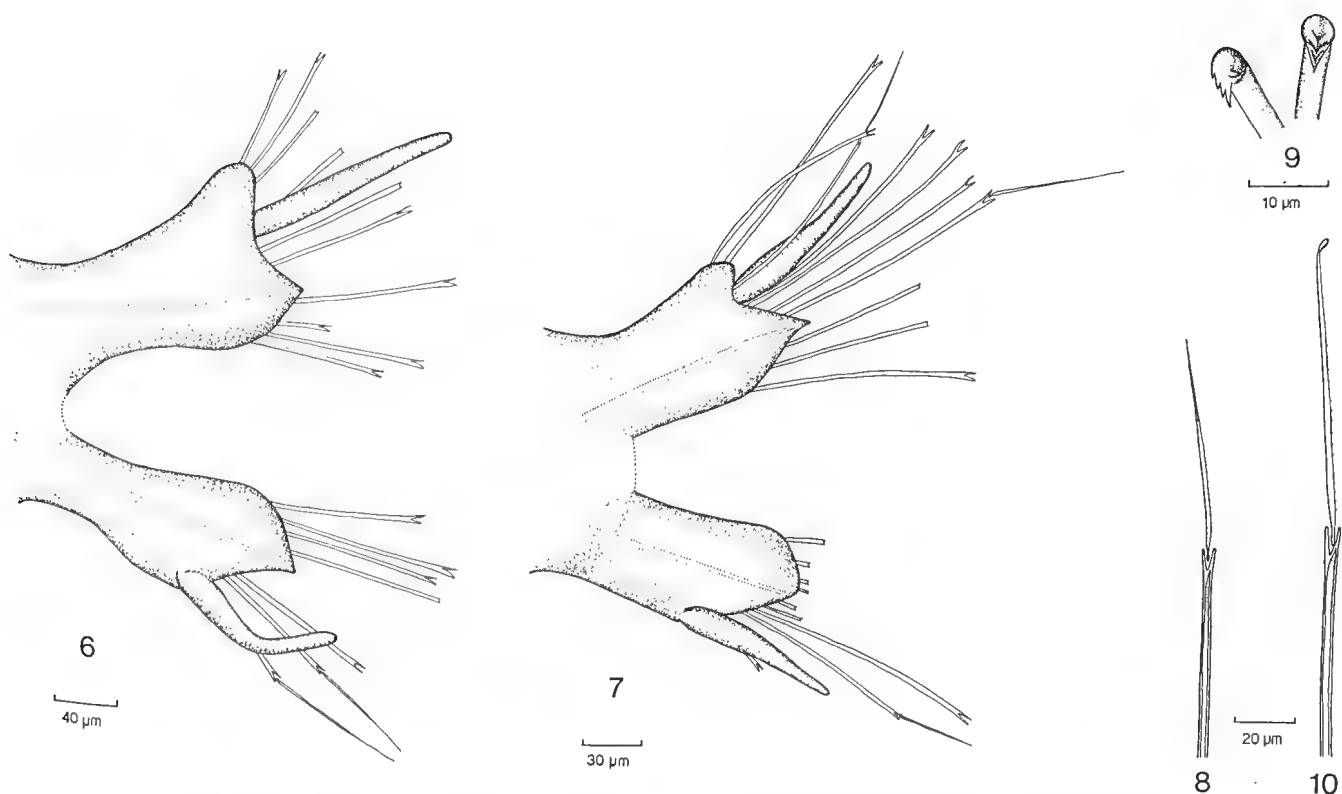
Description. Length of male 3.6 mm (22 setigers), females up to 5.8 mm (24 setigers). Prostomium rounded, with pair of ventral palps and 2 pairs of eyes with lenses. Four pairs of biarticulated tentacular cirri, with diameter of terminal article less than half that of basal; two posterior pairs slightly longer than two anterior pairs, reaching setiger 2–3 (Knox and Cameron, 1970, figs 1–3). Pair of sexually dimorphic jaws (see below). Paragnaths observed only in juvenile; numerous conical oral paragnaths, presumably crown-shaped in adults; maxillary paragnaths consisting of 2 bars, each with a denticle. Biramous parapodia may be ciliated; dorsal cirri larger and inserted more distally than ventral cirri (Fig. 11). Homogomph spinigers, shafts without septa, blades coarsely serrated (Banse, 1977a, pl. 1:figs h, i). Pygidium with pair of subulate anal cirri.

Male characteristics. Jaws of prolonged type with 3 proximal teeth (Fig. 12). No copulatory hooks. Epitokous male with accessory cirri on ventral side of notopodia and dorsal side of neuropodia (Fig. 11), and about 20 homogomph spinigers and 5 simple capillary setae per fascicle.

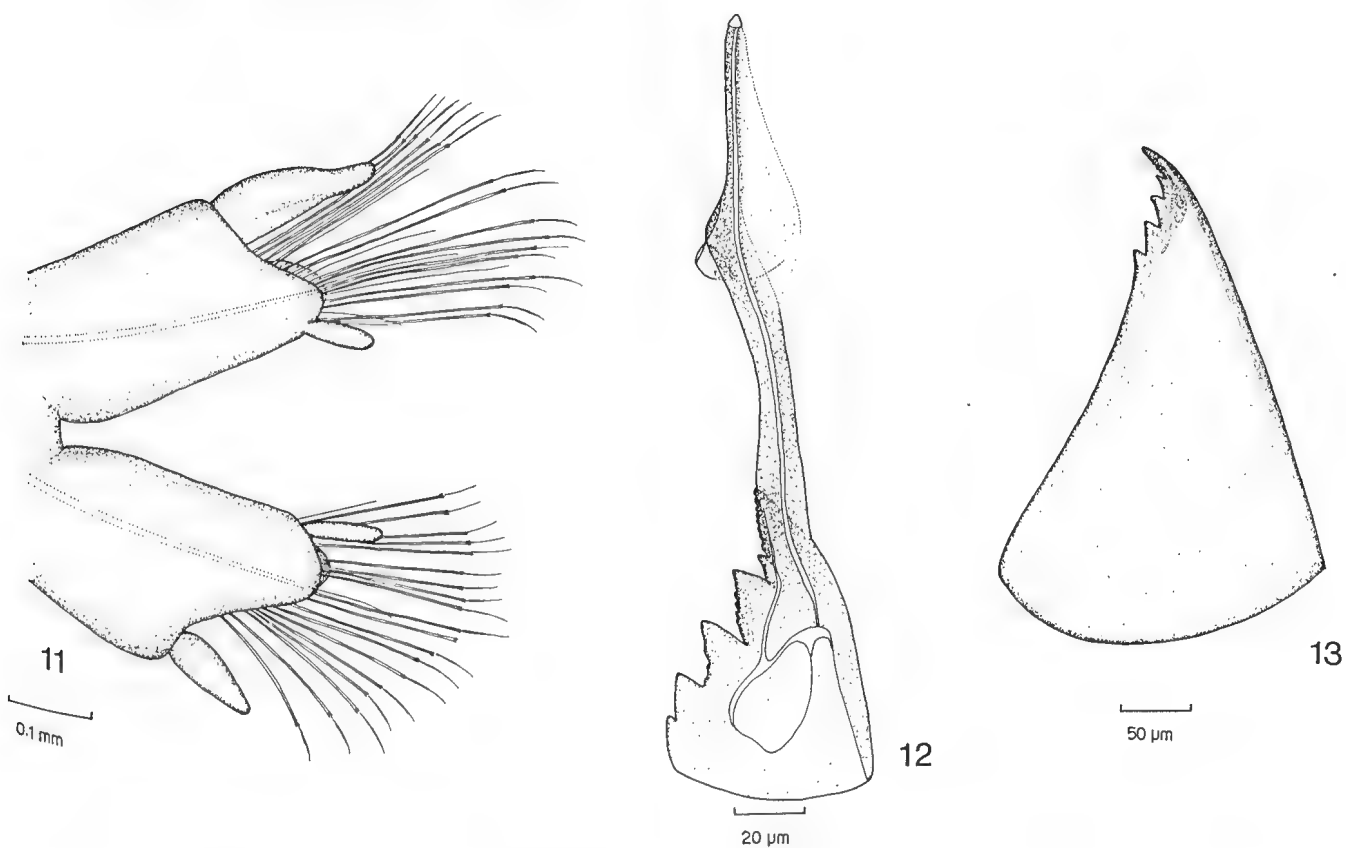
Female characteristics. Jaws of shortened type with 3–4 teeth (Fig. 13). Accessory parapodial cirri absent. About 5–10 homogomph spinigers per fascicle; simple setae absent. Bulbous lobe at base of dorsal cirrus (presumably associated with gonopore).

Biology. The smallest juveniles lacked the anterior two pairs of tentacular cirri and possessed setae associated with the fourth pair as is typical for larval nereidids. The male specimen contained sperm morulae and free spermatozoa.

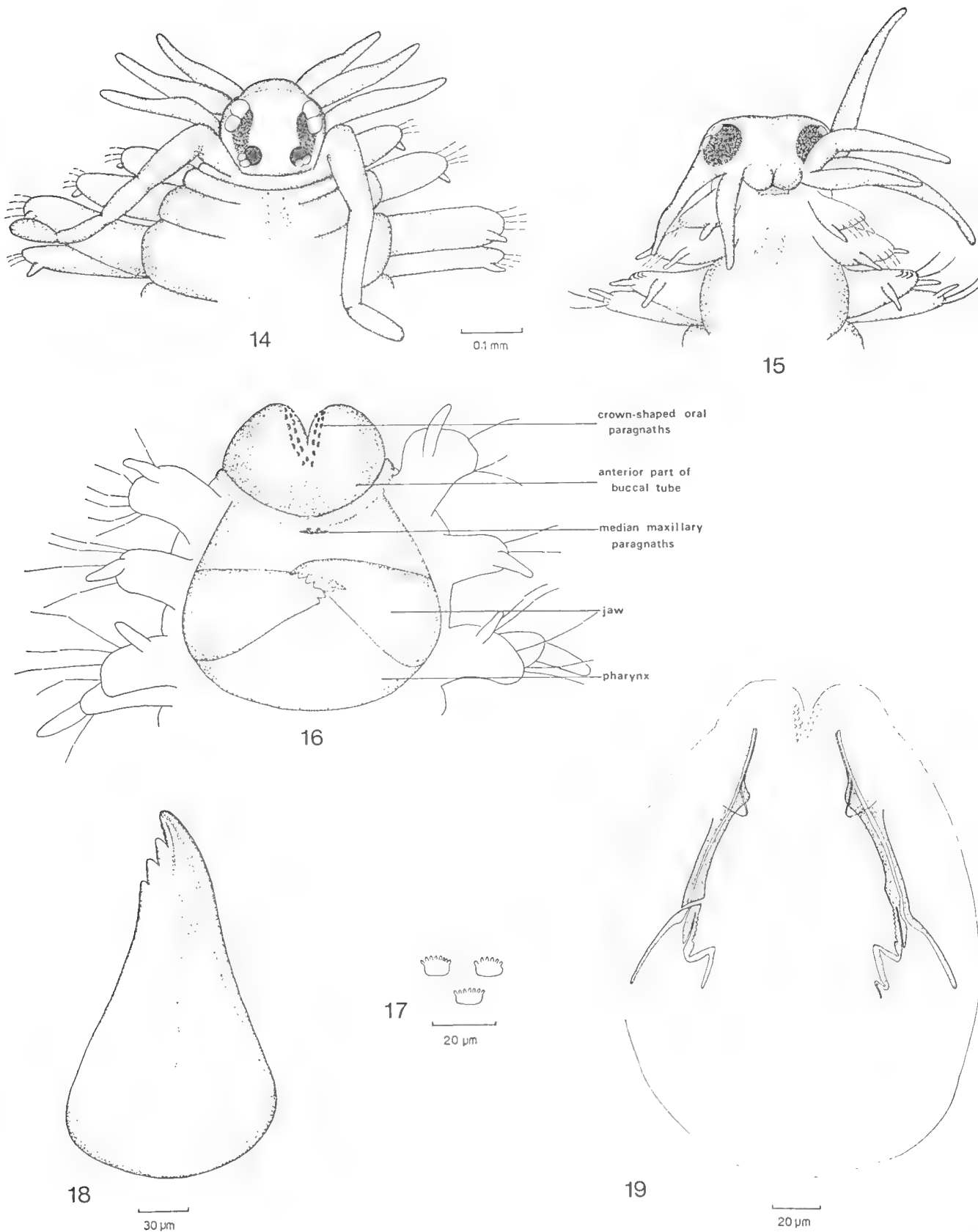
Distribution. Snares Island, New Zealand (Fig. 1).



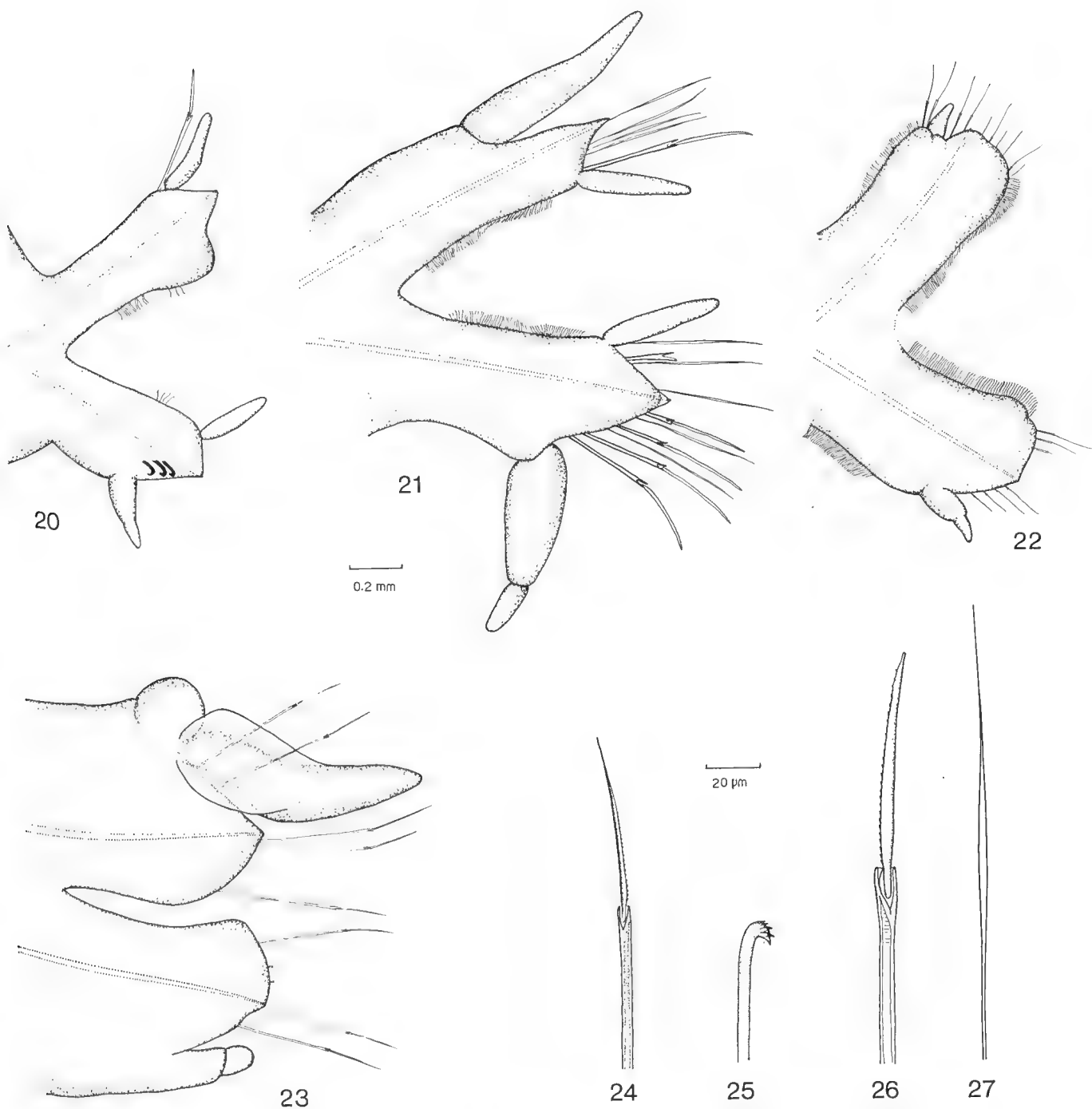
Figs 6–10. *Micronereis piccola*, n.sp. (continued). 6, parapodium of male from setiger 10, anterior view; 7, parapodium of female from setiger 7, anterior view; 8, compound spiniger from setiger 7; 9, copulatory hooks from setiger 3; 10, compound falciger from setiger 7. [6, 9, 10 holotype (USNM 54514); 7, 8 paratype 1 (USNM 60505).]



Figs 11–13. *Micronereis minuta*. 11, parapodium of male from setiger 12, anterior view; 12, jaw of male; 13, jaw of female. [11, 12 specimen 2; 13 specimen 3 (CM AQ3505).]



Figs 14–19. *Microneireis bansei*. 14, anterior end of female, dorsal view (AMS W.17183); 15, same of male, ventral view (AMS W.17186); 16, same of female showing everted anterior buccal tube, ventral view (WAM); 17, oral paragnaths (WAM); 18, jaw of adult (USNM 60512); 19, jaws of juvenile (distal prolongation of one side fractured) (AMS W.17189).



Figs 20-27. *Micronereis bansei* (continued). 20, parapodium of male from setiger 3, anterior view (dorsal accessory cirrus lost); 21, same of male from setiger 12, anterior view; 22, same of female from setiger 3, anterior view; 23, same of female from setiger 12, anterior view; 24, compound spiniger from setiger 12; 25, copulatory hook from setiger 3 of male; 26, compound falciger from setiger 12 of male; 27, simple seta from same.
[20, 21 (AMS W.17186); 22 (AMS W. 17183); 23 (AMS W. 17184); 24 (AMS W.17184); 25-27 (AMS W.17186).]

***Micronereis bansei* (Hartmann-Schröder), n. comb.**
Figs 1, 14-27

Micronereis variegata (non Claparède, 1863).—Fauvel, 1927: 433, fig. 107.—Gravier, 1934:351, fig 3.
Quadricirra sp.—Banse, 1977a:127, pl. 2, figs b, d.
Quadricirra bansei Hartmann-Schröder, 1979:121, figs 227-237 (Broome, Western Australia).

Material examined. AUSTRALIA: *Western Australia*: Broome, Gantheaume Point, 24 September 1975, G. Hartmann-Schröder and G. Hartmann, collectors—1 ♂ and 2 ♀♀ (WAM). *Queensland*: Lizard Island, 100 m off E end of Mangrove Beach, 14°40'49"S, 145°28'00"E, sandy bottom with drift algae (*Lyngbya majuscula*) and diatomaceous material, 3 m, 30 September 1978, A. Jones and C. Short, collectors—1 ♂ (AMS W.17179-81) and 4 ♀♀ (AMS W.17182-5, USNM 60512). Lizard Island, 200 m SW off

Freshwater Beach, 14°41'00"S, 145°27'28"E, 3 m, 10 October 1978, A. Jones and C. Short, collectors—1 ♂ (AMS W. 17186) and 1 juvenile (AMS W. 17187-8). Lizard Island, 1.6 km SW off Eagle Island, in sediment from coral fans, rubble and dead coral on reef face and bommies, 4.6-7.6 m, 17 October 1978, J. Lowry and P. Terrill, collectors—1 juvenile ♀ (AMS W. 17189). One Tree Island, 60 m SW from sand spit, Shark Alley, sandy bottom, 1.5 m, 15 October 1979, C. Short and J. Young, collectors—1 ♀ (AMS W. 17190). *New South Wales*: Gunnamatta Bay, Port Hacking, 34°03'25"S, 151°08'53"E, coarse sandy bottom, 1.5 m, 8 January 1975, S. Rainer and A. Bothwell, collectors—1 juvenile ♀ (AMS W. 17191).

EGYPT: Suez Canal, Port Said—1 ♂ (BM 1926:11:12:30).

Diagnosis. Jaws of shortened type in adults of both sexes. Spinous copulatory hooks and accessory parapodial cirri present in male epitokes, absent in females. Homogomph spinigers with weak septa in shaft, finely serrated spinigerous blades in females and atokous males, replaced by falcigers and simple setae in epitokous males.

Description. Length of males up to 2.1 mm (20 setigers), females up to 3.8 mm (22 setigers). Prostomium rounded with pair of ventral palps and 2 pairs of eyes with lenses (Figs 14, 15). Four pairs of tentacular cirri, posterior pair longest, reaching setiger 4-5 in some specimens (Fig. 14). Oral paragnaths crown-shaped with 6-8 cusps (Figs 16, 17); maxillary paragnaths 2 bars each with irregularly shaped denticle; pair of jaws with prolonged distal part in juveniles (Fig. 19) and shortened type with 3-4 teeth in adults of both sexes (Figs 16, 18). Parapodia with cilia, simple dorsal cirrus and more or less biarticulated ventral cirrus (Figs 20-22). Slender homogomph spinigers, shafts with weak septa (visible with 1000× magnification), blades finely serrated (Fig. 24). Some specimens with segmental eyespots. Pygidium with pair of anal cirri of varying length.

Male characteristics. Setiger 3 with 3 neuropodial copulatory hooks each with 4-6 spines (Figs 20, 25). Epitokal changes consisting of (1) accessory cirri appearing on ventral side of notopodia and dorsal side of neuropodia (figs 20, 21) and (2) spinigers being replaced by falcigers (fig. 26) and simple setae with widened middle portion (fig. 27).

Female characteristics. Accessory parapodial cirri absent. No obvious change of setae associated with sexual maturity. In mature females dorsal cirri enlarged, with lamellar extensions and bulbous lobe at base (presumably associated with gonopore) (Fig. 22).

Biology. Two of the females were collected inside their mucous cocoons, measuring 1.4 and 1.6 mm in diameter; they contained approximately 150 and 190 pink eggs, 100 µm in diameter.

Remarks. The specimen from Port Said was reported by Fauvel (1927), who remarked that it was obviously a male, having jaws with long appendages and copulatory hooks. He discussed and illustrated the accessory cirri in a middle parapodium and stated that he had not found such cirri on any of the other

specimens in his collection. Although he concluded that the specimen might represent a new species, he chose to report it as *M. variegata* for the time being.

Banse (1977a) re-examined and figured the poorly preserved specimen. He referred it to *Quadricirra* sp. indicating that the features were insufficient for a complete diagnosis. Upon re-examination in the course of the present study, the specimen was identified as *M. bansei*. The jaws were dissected out and found to be of the shortened type, contrary to the statement of Fauvel (1927). The shafts of the compound setae are faintly septate. There are fine atokous spinigers and thicker epitokous falcigers, typical for *M. bansei*. The transformation of this specimen had not yet reached the stage where simple setae appear.

Distribution. Western Australia, Queensland and New South Wales, Australia; Port Said, Egypt (Fig. 1).

Micronereis nanaimoensis Berkeley and Berkeley Figs 1, 28-30

Micronereis variegata (non Claparède, 1863).—Ramsay, 1914:243, figs 2-5, 7.—Berkeley, 1924:290.—Berkeley and Berkeley, 1948:60, fig. 89.

Micronereis nanaimoensis Berkeley and Berkeley, 1953:85, pls 1, 2 (Departure Bay, British Columbia).—Reish, 1961:276.—Pettibone, 1967:6.—Banse and Hobson, 1974:69, fig. 18h.—Banse, 1977a:122, pl. 1:figs a-d.

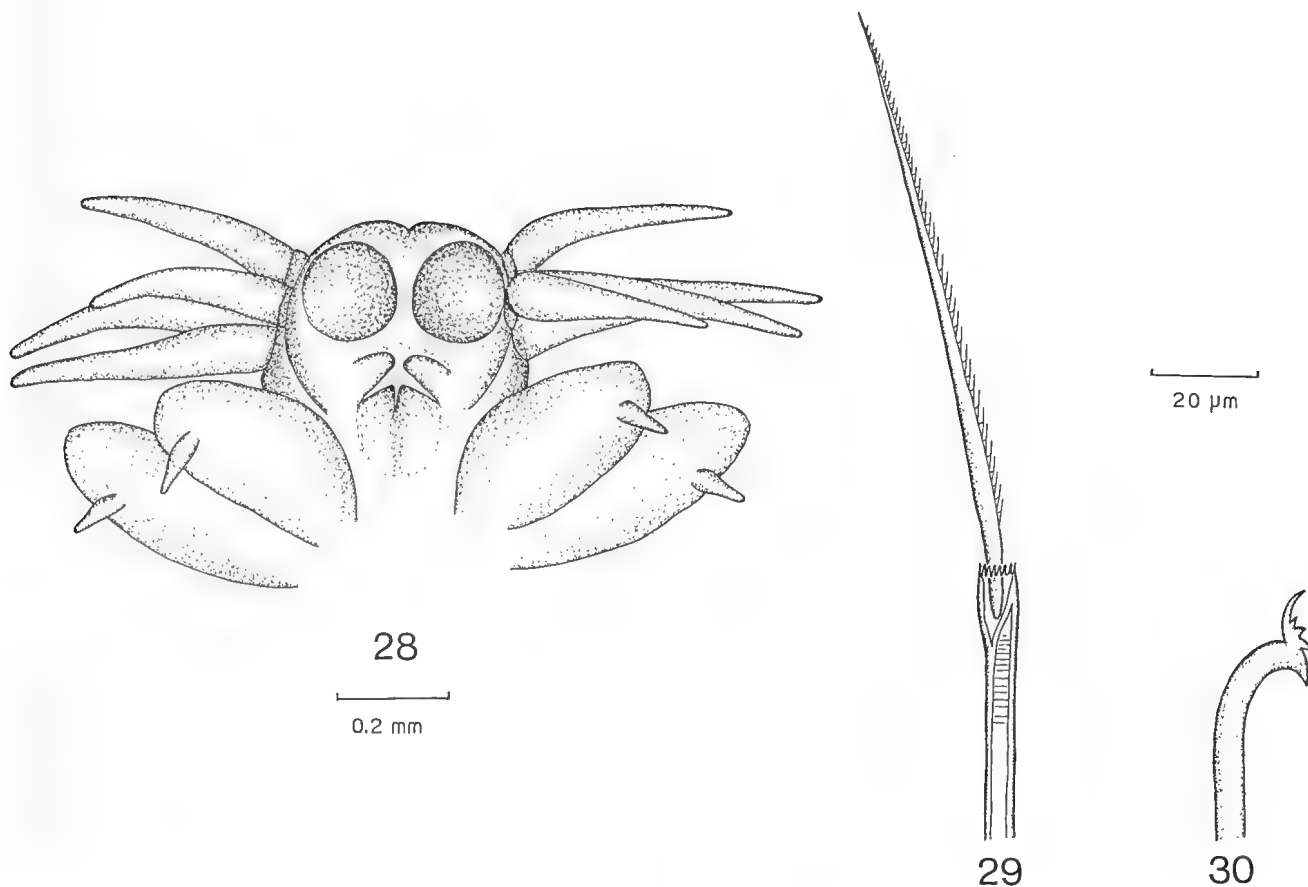
Phyllodocella bodegae Fauchald and Belman, 1972:107, figs 2 (Bodega Bay, California).—Banse, 1977a:124.

Material examined. CANADA: British Columbia, Departure Bay, 23 April to 23 May 1947, E. and C. Berkeley, collectors—1 ♂ and 3 ♀ SYNTYPES (AMS W. 17175-8, from USNM 32855-6).

Diagnosis. Jaws of shortened type in both sexes. Accessory parapodial cirri absent. Mouth with conical lateral lips. Crested copulatory hooks present in males. Homogomph spinigers; shafts with distinct septa, serrated blades, epitokous males with additional simple setae.

Description. Length of males up to 13 mm (23 setigers), females up to 15 mm (26 setigers). Prostomium rounded to quadrate with pair of ventral palps and 2 pairs of eyes with lenses. Four pairs of short, subulate tentacular cirri. Mouth with conical lateral lips (Fig. 28). Oral paragnaths crown-shaped with 5 cusps (Banse, 1977a, pl. 1:fig. a); maxillary paragnaths not observed; pair of jaws of shortened type in both sexes with 3-4 teeth (Berkeley and Berkeley, 1953, pl. 1:fig. 3). Parapodia strongly ciliated, biramous from setiger 3, with small dorsal and ventral cirri; homogomph spinigers; shafts with distinct septa and distally crenulated; blades serrated, each serration ending in distinct hair-like extension (Fig. 29). Pygidium with pair of anal cirri.

Male characteristics. Setiger 3 with 5 or more crested neuropodial copulatory hooks (fig. 30). Setae of epitokes include spinigers and additional simple setae with widened middle portion.



Figs 28–30. *Micronereis nanaimoensis*. 28, anterior end, setae omitted, ventral view; 29, compound spiniger from setiger 11; 30, copulatory hook from setiger 3.
[28 (AMS W.17175); 29, 30 (AMS W.17178).]

Female characteristics. Parapodia greatly inflated but dorsal cirri small throughout length of body. Bulbous lobe at base of dorsal cirrus (presumably associated with gonopore). No obvious change of setae associated with sexual maturity.

Biology. Reproduction and development of *M. nanaimoensis* has been described by Berkeley and Berkeley (1953).

Remarks. Fauchald and Belman (1972) described *Phyllodoce bodegae* from Bodega Harbor, California on the basis of a single female found in a mucous cocoon. Banse (1977a) referred the species to *Micronereis*. It is relatively large (8 mm for 24 setigers) and has conical lateral lips, inflated parapodia with small dorsal and ventral cirri, and homogomph spinigers that have distally crenulated, septate shafts and serrated blades with hair-like extensions (Fauchald and Belman, 1972, figs 1, 2). All these characters agree with *M. nanaimoensis*. Although the type specimen of *M. bodegae* cannot be located (Kudenov, pers. comm.), the information available is sufficient to demonstrate that *M. bodegae* is a junior synonym of *M. nanaimoensis*.

Distribution. British Columbia, Canada; Washington and California, U.S.A. (Fig. 1).

Micronereis halei Hartman Figs 1, 31–33

Micronereis halei Hartman, 1954:25, figs 18–21 (South Australia).—Reish, 1961:276.

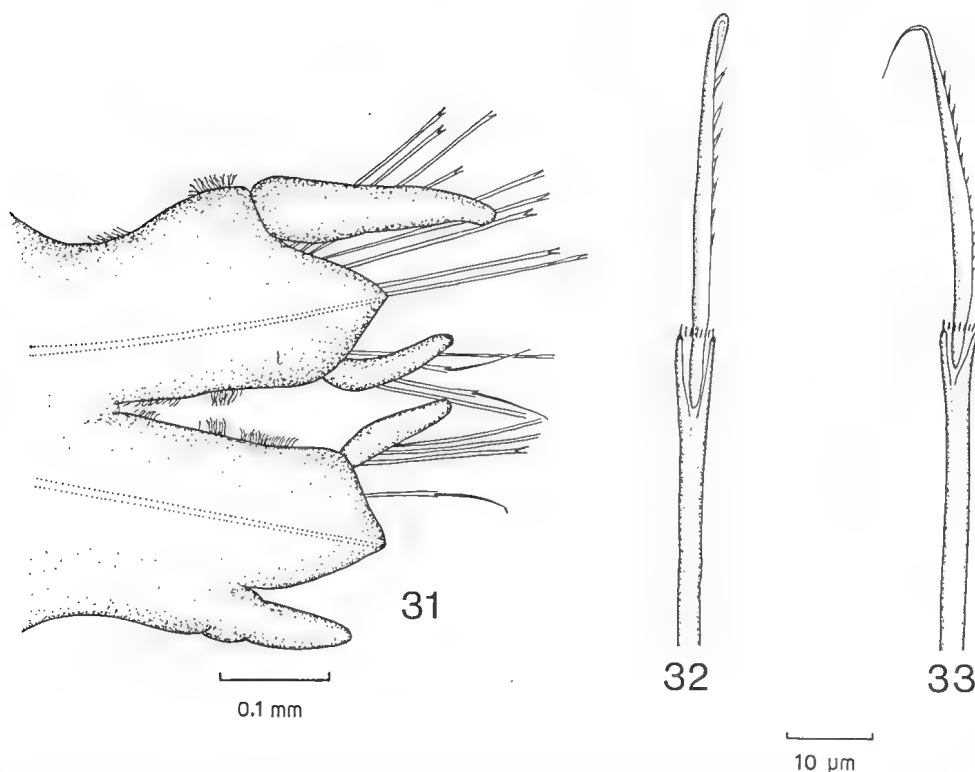
Micronereis sp. 1 Poore *et al.* 1975:27, 50.

Quadricirra halei.—Banse, 1977a:126, pl. 2:figs a, c.

Material examined. AUSTRALIA: *South Australia*: Sellick Beach, at outer edge of reef, from stones on rock pools, 16 January 1936, H.M. Hale and K. Sheard, collectors—10 SYNTYPES (1 ♂ AHF Poly 843; 3 ♂♂ AHF Poly 844; 2 ♂♂ and 1 juvenile AHF n 1008; 2 ♂♂ AHF n 7645; 1 juvenile AHF n 7647). *Victoria*: Port Phillip Bay, c. 38°21'S, 144°51'E, PPBES sta. 985, 9 m, 9 December 1971—1 juvenile (NMV 8164).

Diagnosis. Jaws of males, and presumably females, of shortened type. Male epitokes with accessory parapodial cirri, without copulatory hooks. Homogomph spinigers; shafts without septa; blades finely serrated in male atokes; spinigers and falcigers in male epitokes.

Description. Length of males up to 6.7 mm (27 setigers). Prostomium rounded, with pair of ventral palps and 2 pairs of eyes with lenses (Hartman, 1954, fig. 18). Four pairs of weakly biarticulated tentacular



Figs 31-33. *Micronereis halei*. 31, parapodium of male from setiger 12, anterior view; 32, compound falciger from setiger 12 of male; 33, compound spiniger with fine distal tip from setiger 12 of male. [31 (AHF n 1008); 32, 33 (AHF Poly 0844).]

cirri; anterior 2 pairs shorter, posterior 2 pairs reaching setiger 3. Oral and maxillary paragnaths not observed; pair of jaws of shortened type in both sexes with 4-5 teeth (Hartman, 1954, fig. 19). Parapodia may be ciliated; dorsal cirri of biramous parapodia larger than ventral cirri (Fig. 31). Homogomph spinigers, shafts without septa, blades finely serrated, of varying length. Segmental eyespots present in one specimen (NMV 8164). Pygidium with pair of anal cirri.

Male characteristics. No copulatory hooks. Accessory cirri attached ventrally on notopodia and dorsally on neuropodia (= digitate lobes in Hartman, 1954, fig. 20). Setae of epitokes consisting mostly of falcigers (Fig. 32) and some spinigers with fine distal tips, often bent (Fig. 33); serrations on blades stronger than in atokes.

Female characteristics. No adult females were available for examination.

Biology. Eight of the 10 syntypes examined contained male gametes. Accessory parapodial cirri were absent in the smaller specimens; one syntype (AHF Poly 844, measuring 4.1 mm in length for 23 setigers) with very short accessory cirri and few falcigers was thought to be in the early stages of epitoky.

Distribution. South Australia and Victoria, Australia (Fig. 1).

Micronereis eniwetokensis Reish

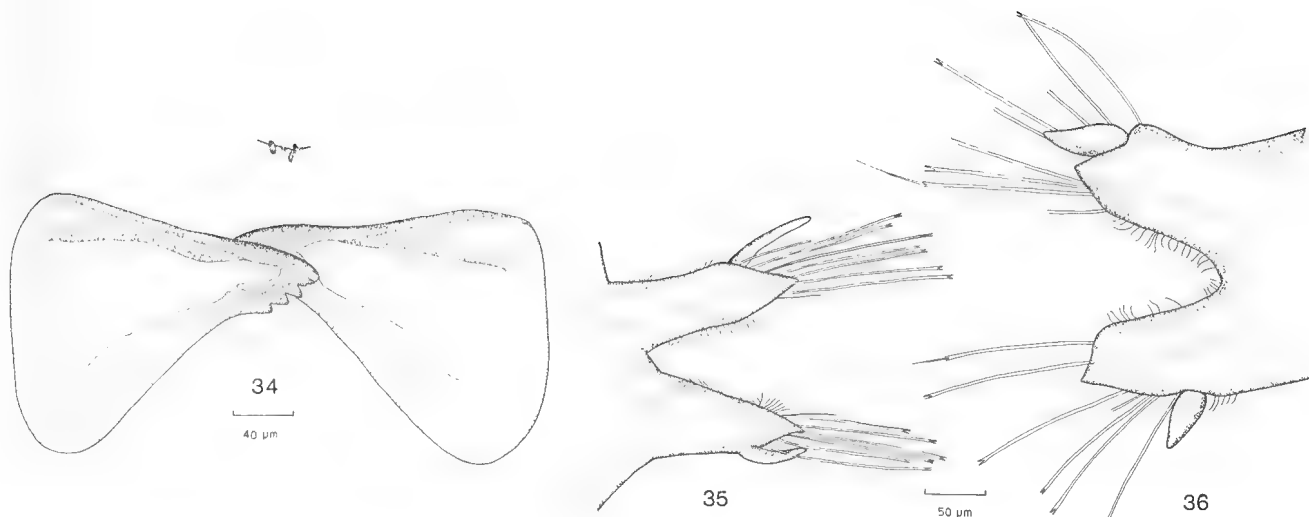
Figs 1, 34-36

Micronereis eniwetokensis Reish, 1961: 273, figs 2-6 (Eniwetak Atoll, Marshall Is).—Banse, 1977a:122.

Material examined. *Marshall Islands:* Eniwetak Atoll: Aaraanbiru I., intertidal, 4 September 1956, D.J. Reish, collector—♀ HOLOTYPE (USNM 30404) and 1 ♀ PARATYPE (USNM 30405). Igurin I., 27 August 1956, D.J. Reish, collector—1 ♀ (USNM 30406). Parry I., 30 m, 14 September 1957, M. Chamberlain, collector—1 ♂ (USNM 30407).

Diagnosis. Jaws of shortened type in both sexes. Accessory parapodial cirri and copulatory hooks absent. Homogomph spinigers with septate shafts, blades finely serrated.

Description. Length of female 1.8 mm (18 setigers), male 1.7 mm (14 setigers). Prostomium rounded, with pair of ventral palps and 2 pairs of eyes with lenses, posterior pair smaller and lenses not as obvious as in anterior pair. Four pairs of subulate tentacular cirri, short in female specimens, longer in male, reaching to end of setiger 3. Oral paragnaths not observed; median maxillary paragnaths consisting of 2 light bars, each with dark, irregularly shaped denticle; paired jaws of shortened type in both sexes, with 3 teeth and bulbous basal part (Fig. 34). Biramous parapodia with notopodia and neuropodia each with single yellow aciculum (not black, as stated by Reish, 1961); heavy ciliated; weakly subulate dorsal and ventral cirri (Figs 35, 36).



Figs 34–36. *Micronereis eniwetokensis*. 34, jaws and median maxillary paragnaths; 35, parapodium of male from setiger 6, anterior view; 36, parapodium of presumed female from setiger 8, anterior view. [34, 36 paratype (USNM 30405); 35 (USNM 30407).]

Homogomph spinigers, shafts with weak septa, blades finely serrated. One specimen (USNM 30407) with segmental eyespots.

Male characteristics. Male slender, with few setigers; no epitokal changes observed.

Female characteristics. More inflated appearance and higher number of setigers.

Distribution. Eniwetak Atoll, Marshall Islands (Fig.1).

Key to the Species of *Micronereis* (Males only)

1. Males with prolonged type of jaws (Fig. 2) 2
 - Males with shortened type of jaws (Fig. 18) 4
2. Males without copulatory hooks on neuropodia of setiger 3; epitokous males with accessory cirri on lower part of notopodia and upper part of neuropodia (Fig. 11) *M. minuta*
 - Males with copulatory hooks (Fig. 9); epitokous males without accessory parapodial cirri (Fig. 6) 3
3. Shafts of spinigers with septa (Fig. 8); prolonged male jaws without proximal teeth (Fig. 5) *M. piccola*, n.sp.
 - Shafts of spinigers without septa; prolonged male jaws with proximal teeth (Fig. 2) *M. variegata*
4. Males with copulatory hooks on neuropodia of setiger 3 (Figs 25, 30); epitokous males with simple setae (Fig. 27) 5
 - Males without copulatory hooks; epitokous males without simple setae 6
5. Epitokous males with accessory cirri on lower part of notopodia and upper part of neuropodia (Fig. 21); copulatory hooks with spines (Fig. 18) *M. bansei*
 - Epitokous males without accessory parapodial cirri; copulatory hooks crested (Fig. 30) *M. nanaimoensis*
6. Epitokous males with accessory cirri on lower part of notopodia and upper part of neuropodia (Fig. 31) and some falcigers (Fig. 32) *M. halei*
 - Epitokous males without accessory parapodial cirri (Fig. 35) and only spinigers *M. eniwetokensis*

DISCUSSION

The Nereididae is one of the most uniform polychaete families. Of the four subfamilies, the Notophycinae departs most widely from the basic nereidid plan. Banse (1977a) discussed the taxonomic position of the Notophycinae and concluded that, although they are the most aberrant, they belong to the Nereididae. He considered the seta, particularly the internal septa and the structure of the distal end of the shaft, as the strongest evidence. Notophycines were regarded as primitive nereidids (Ramsay, 1914), but Banse (1977a: 132) stated that "the evidence which has become available since his study has not provided unambiguous evidence".

The notophycines display a curious mixture of epitokous characters retained from their nereidid relatives, and specializations acquired as members of the meiofauna. The epitokal modifications in females consist only of enlargement of eyes, parapodia and dorsal and ventral cirri. Male modifications range from enlarged eyes in *Micronereis variegata* to the possession of accessory parapodial cirri and the addition and replacement of spinigers by simple setae and falcigers as in *M. bansei*.

Reproductive adaptations common to the meiofauna in general are related to the relatively small number of gametes that small animals can produce, and include copulation, hermaphroditism, the formation of egg cocoons and brood protection (Swedmark, 1971). Reproduction and development have been studied in detail for two species of *Micronereis*: *M. nanaimoensis* by Berkeley and Berkeley (1953) and *M. variegata* by Racovitza (1893) and Rullier (1954). Both species undergo an extended courtship and spawning behaviour. The meiofaunal specializations consist of copulatory hooks in the male, a slightly larger body in the female, relatively large and few eggs, construction of a mucous cocoon, brood protection and care by the female, and direct development of the young. The combination of more developed epitokal modifications in the males and the reproductive meiofaunal adaptations has led to a pronounced sexual dimorphism.

Antennae are absent in Notophycinae at all stages of development. Antennae are present in all other subfamilies and develop early in the 3-setiger larva of *N. diversicolor* (Dales, 1950). The absence of antennae in Notophycinae is a unique character among the Nereididae, suggesting that the notophycines represent either the most ancestral or the most derived subfamily. In view of the fact that the most closely related families, the Hesionidae and Syllidae (Dales, 1962) are characterized by the possession of antennae, it is probable that their absence in the Notophycinae

represents a derived state and that they are the most derived subfamily of Nereididae.

The species of *Micronereis* display a mosaic of characters (Table 1). The prolonged type of jaw is found in males of *M. variegata*, *M. piccola*, and *M. minuta*, while the males of the remaining four species, *M. bansei*, *M. nanaimoensis*, *M. halei* and *M. eniwetokensis*, have jaws of the shortened type. Rullier (1954) has shown that the prolonged jaw of *M. variegata* develops in young male and female individuals. When the females reach about 16 setigers, the prolongation breaks off at a predestined place (Fig. 2) and the jaw enlarges proximally, while the males retain the distal prolongation. The prolonged jaws were observed in juvenile females of *M. minuta* and *M. piccola*. An interesting find was the presence of prolonged jaws in a juvenile specimen of *M. bansei* (Fig. 19), which belongs to the group of species where both adult males and females have the shortened type of jaws. This indicates that the prolonged type develops first in both groups of species and the shortened jaw of both sexes is a derived condition.

Accessory parapodial cirri are found in mature males of *M. bansei*, *M. minuta* and *M. halei*, while they are absent in the remaining four species. The males of four species have copulatory hooks; their shape is similar in *M. variegata*, *M. piccola*, and *M. bansei*, but more elaborate in *M. nanaimoensis*.

The type of jaw and presence or absence of accessory parapodial cirri and copulatory hooks cannot be correlated and thus cannot be used to divide the genus into species groups. It appears that the transformation from the prolonged to the shortened type of jaw occurred primitively only in females, but may have been adopted by males more than once independently. It is presumed that accessory cirri and copulatory hooks evolved only once in *Micronereis* and thus their absence should represent the ancestral, and their presence the derived, character state. However, both characters may have been lost independently more than once, and the relationships within *Micronereis* are unclear.

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Note Added in Proof

While this paper has been in press, *Micronereis ochotensis* Buzhinskaya has been described from the Sea of Okhotsk, U.S.S.R.

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Epipontonia anceps n. sp., a Sponge-associated Pontoniine Shrimp from Heron Island, Queensland. (Crustacea: Decapoda: Palaemonidae)

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ABSTRACT. A second species of the pontoniine shrimp genus *Epipontonia* Bruce, 1977, is described and illustrated. *Epipontonia anceps* n. sp. is an associate of a sponge of the genus *Dysidea* found at Heron Island, Queensland at a depth of 18 m. *E. anceps* may be distinguished from *E. spongicola* Bruce, the only other species of the genus, by the absence of an antennal spine and the presence of large unequal chelae on the second pereopods.

BRUCE, A.J., 1983. *Epipontonia anceps* n. sp., a sponge-associated pontoniine shrimp from Heron Island, Queensland. (Crustacea: Decapoda: Palaemonidae). Records of the Australian Museum 35(1): 19-28.

The pontoniine genus *Epipontonia* (Palaemonidae, Samouelle, 1819) is represented by a single species *E. spongicola*, described from a single specimen from Wasin Island, Kenya (Bruce, 1977), where it was found in association with a sponge at a depth of 12 m. There have been no subsequent records of this species in the literature. Recently several examples of a closely related species of shrimp were found in association with a sponge at Heron Island, in the Capricorn Islands, near the southern end of the Great Barrier Reef. These specimens differ from *E. spongicola* in several characteristic morphological features and they are now described as a new species.

SYSTEMATICS

Epipontonia anceps n. sp. Figs 1-10

Material examined. 3 ovigerous ♀♀, 1 juvenile, Heron Island, Queensland 23° 28.0'S, 151°59.2'E, 18 m, 17 September 1979, coll. L. Owens and L. Thompson.

Holotype. Ovigerous female, Australian Museum registration number P31485, total length 10.0 mm (approx.); post-orbital carapace length 2.7 mm; length of major chela of second pereopod 5.4 mm; length of minor chela of same 3.6 mm, length of ova 0.5 mm.

Paratypes. (i) Ovigerous female, Rijksmuseum van Natuurlijke Historie, registration number RMNH Crust. D.33340, total length 13.0 mm (approx.); post-orbital carapace length 3.4 mm; length of chela of major second pereopod 5.5 mm, minor chela lacking. (ii) Ovigerous female, post-orbital

carapace length 2.6 mm; major second pereopod lacking, length of chela of minor second pereopod 2.4 mm. (iii) Female, post-orbital carapace length 1.2 mm; chela of major second pereopod 2.0 mm; chela of minor second pereopod 1.0 mm.

Description. A medium-sized pontoniine shrimp, of fairly slender and slightly compressed body form.

The carapace is smooth and with a well-developed rostrum that extends anteriorly to about the level of the distal margin of the lamina of the scaphocerite and slightly exceeds the intermediate segment of the antennular peduncle. The rostrum is acute, strongly compressed, horizontal or slightly depressed, with feebly-developed lateral carinae. The dorsal carina is deep with 6-7 long acute teeth, which increase in size distally to the fifth and then diminish in size; all are situated anteriorly to the level of the orbital notch. The ventral carina is also well developed, with a convex lower border bearing a single slender acute tooth at about 0.6 of its length. The orbit is obsolete. Supra-orbital and hepatic spines are absent. The inferior orbital angle is slightly produced, broadly rounded and almost obsolete, without an antennal spine. An acute para-orbital spine is situated slightly above the inferior orbital angle. The antero-lateral angle of the carapace is slightly produced and bluntly rounded.

The abdominal segments are smooth. The tergite of the first segment is without an antero-dorsal lobe and the third segment is not produced posteriorly. The fourth and fifth segments are about as long as the sixth segment, which is about 1.5 times longer than deep and

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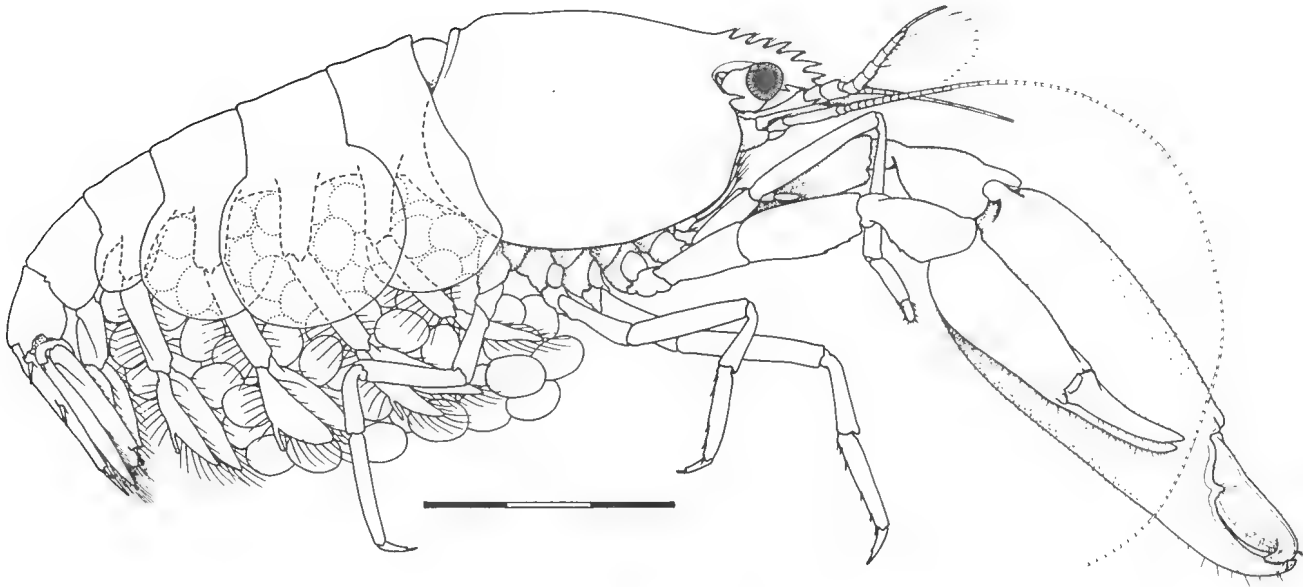


Fig. 1. *Epipontonia anceps* n.sp. Holotype, female, Heron Island, Queensland. Scale in mm.



Fig. 2. *Epipontonia anceps* n. sp., ovigerous female, holotype, Heron Island, Queensland.

broadened, about 1.8 times wider than long. The postero-lateral angle is small and acute and the postero-ventral angle is expanded and acute. The pleura of the

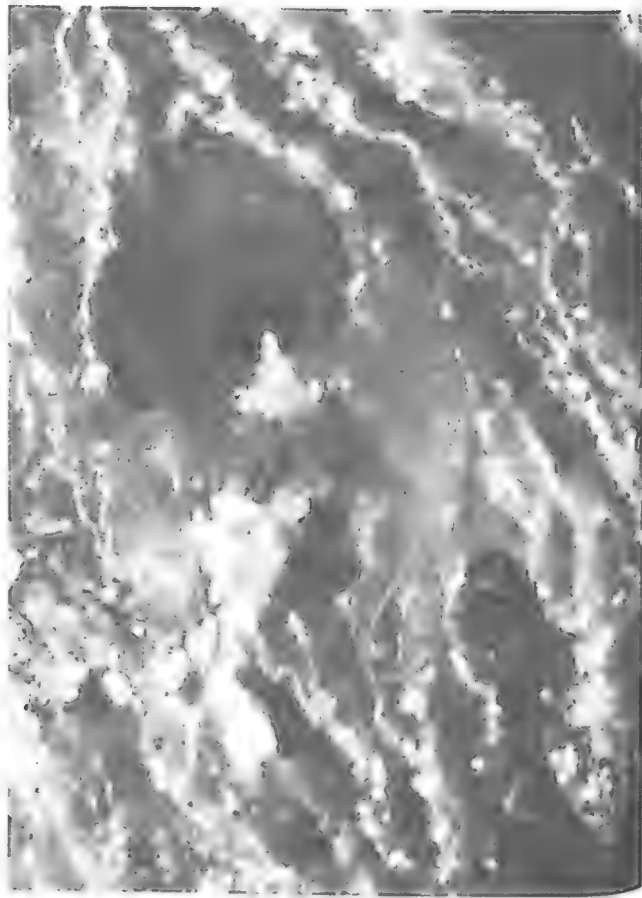


Fig. 3. *Epipontonia anceps* n. sp., ovigerous female *in situ* in host sponge.

first three segments are large and broadly rounded. The fourth and fifth pleura are progressively smaller and also broadly rounded.

The telson is about twice the length of the sixth abdominal segment, 2.1 times longer than wide with

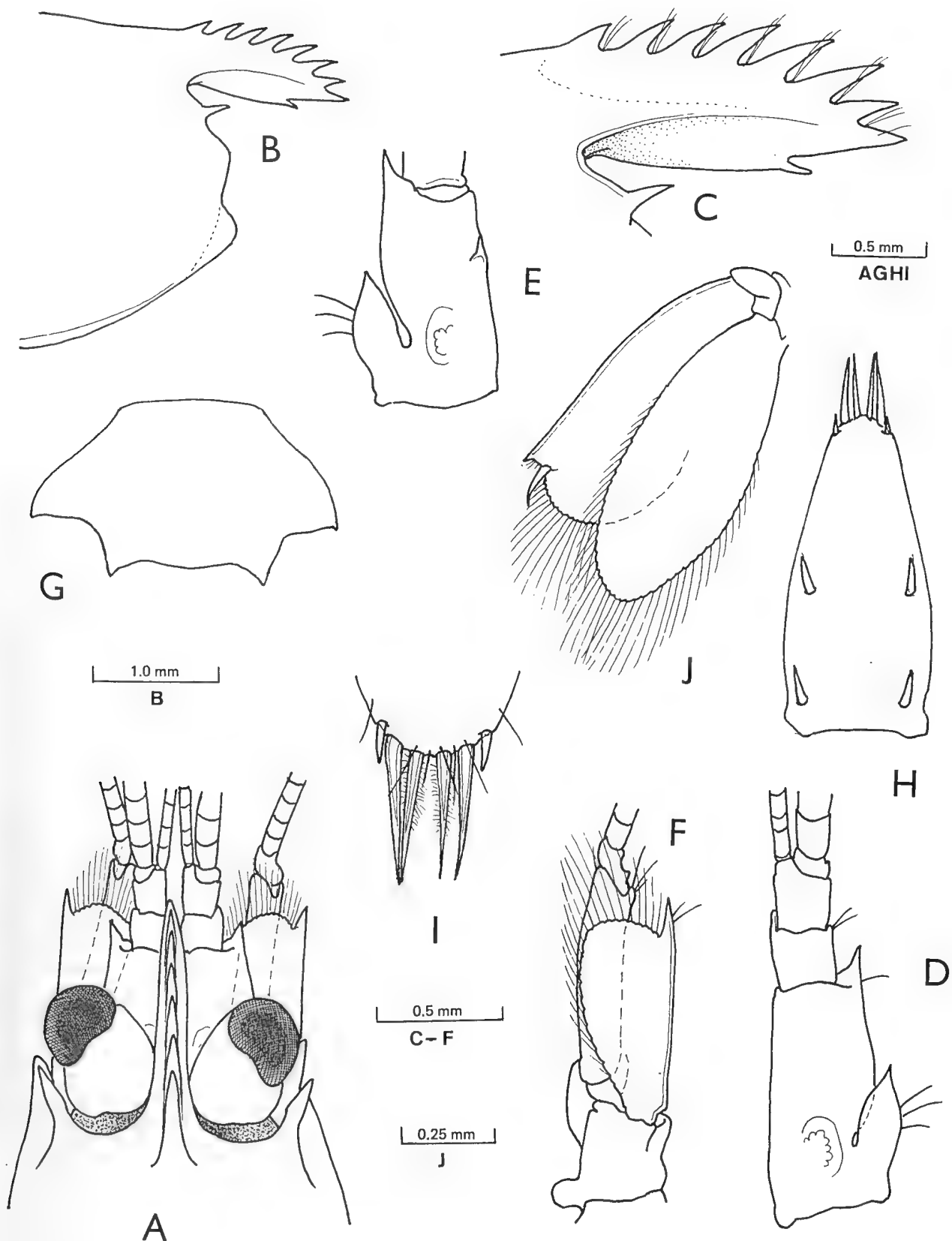


Fig. 4. *Epipontonia anceps* n.sp. Ovigerous female paratype. A, anterior carapace, rostrum and antennae, dorsal. B, anterior carapace and rostrum, lateral. C, rostrum. D, antennule, dorsal. E, antennule, ventral. F, antenna. G, sixth abdominal segment. H, telson. I, posterior telson spines. J, uropod.

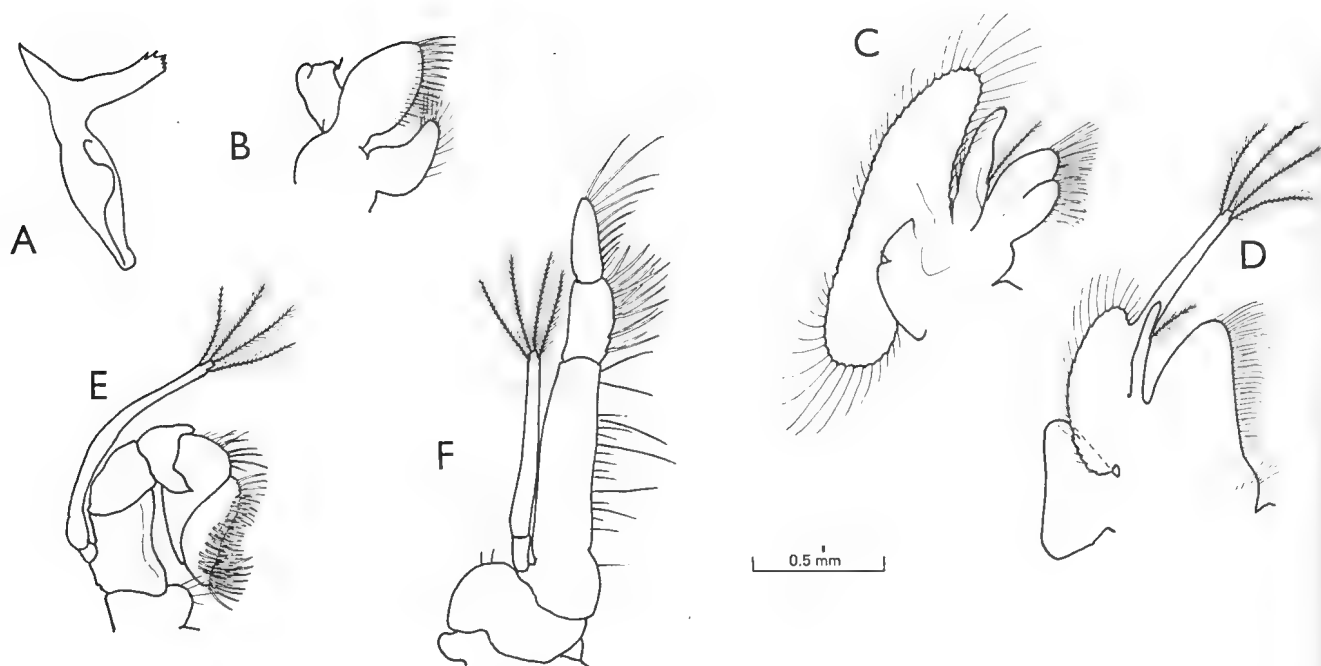


Fig. 5. *Epipontonia anceps* n.sp. Ovigerous female paratype. A, mandible. B, maxillula. C, maxilla. D, first maxilliped. E, second maxilliped. F, third maxilliped.

convex, posteriorly convergent lateral borders; width greatest at one third of length. The dorsal surface bears two subequal pairs of spines, equal to about 0.15 of the telson length, situated remote from the lateral edges at 0.08 and 0.45 of its length. The posterior margin of the telson is rounded, without a medium point, its width equal to 0.4 of the greatest telson width. The lateral spines are small, a little more than half the length of the dorsal spines. The intermediate spines are long, slender and uniformly tapering, about 1.6 times the length of the dorsal spines. The submedian spines are slightly shorter than the intermediates, more slender and finely setulose proximally.

The eyes are well developed, with the cornea globular, situated obliquely on a short stout stalk, which is wider than the diameter of the cornea and rather swollen proximally. No accessory pigment spot is discernible.

The antennulae are rather short. The peduncle exceeds the tip of the spine of the scaphocerite by half the length of the distal segment, and exceeds the tip of the rostrum by most of the distal segment. The proximal segment is about 2.2 times longer than wide. The lateral border is slightly convergent distally and a large disto-lateral lobe is present with an acute lateral tooth reaching beyond the level of the middle of the intermediate segment. A large acute leaf-like stylocerite is present, reaching beyond half the segment length. The statocyst is normal, with a granular statolith. A medial ventral spine is also present at about 0.6 of the length. The intermediate and distal segments are simple, with the distal segment about 1.5 times the length of the intermediate, and slightly more slender, together equal to 0.6 of the length of the proximal segment. The upper

flagellum is biramous, with the 5 proximal segments fused. The short free flagellum consists of a single segment and the longer slender flagellum of five segments. About 12 groups of aesthetascs are present. The lower flagellum is slender and consists of 11–12 segments.

The antenna has a robust basicerite, laterally unarmed but with a large process medially. The ischiocerite and merocerite are normal. The carpocerite is moderately robust, compressed, about 4.5 times longer than wide, slightly bowed and distinctly exceeding the spine of the scaphocerite. The scaphocerite has the lateral border almost straight, terminating distally in a large acute tooth that extends far beyond the anterior margin of the lamina, which is about 2.0 times longer than the maximum width, which lies at about 0.75 of its length; the anterior margin of the scaphocerite is rather truncate. The flagellum is slender, about 3.0 times the post-orbital carapace length.

The mouthparts are similar to those of the type species, differing significantly only in the following features. The incisor process of the mandible is provided with a minute accessory tooth, adjacent to the single acute terminal tooth. The palp of the maxillula has the lower lobe with a non-setiferous ventral tubercle. The palp of the maxilla is more elongate, with a plumose seta arising at one third of the length of the medial margin and the lobes of the endites are more deeply separated. The first maxilliped has a plumose seta on the medial margin of the palp. The second maxilliped has the disto-medial lobe of the carpal segment more acutely pointed. The third maxilliped bears a vestigial arthrobranch.

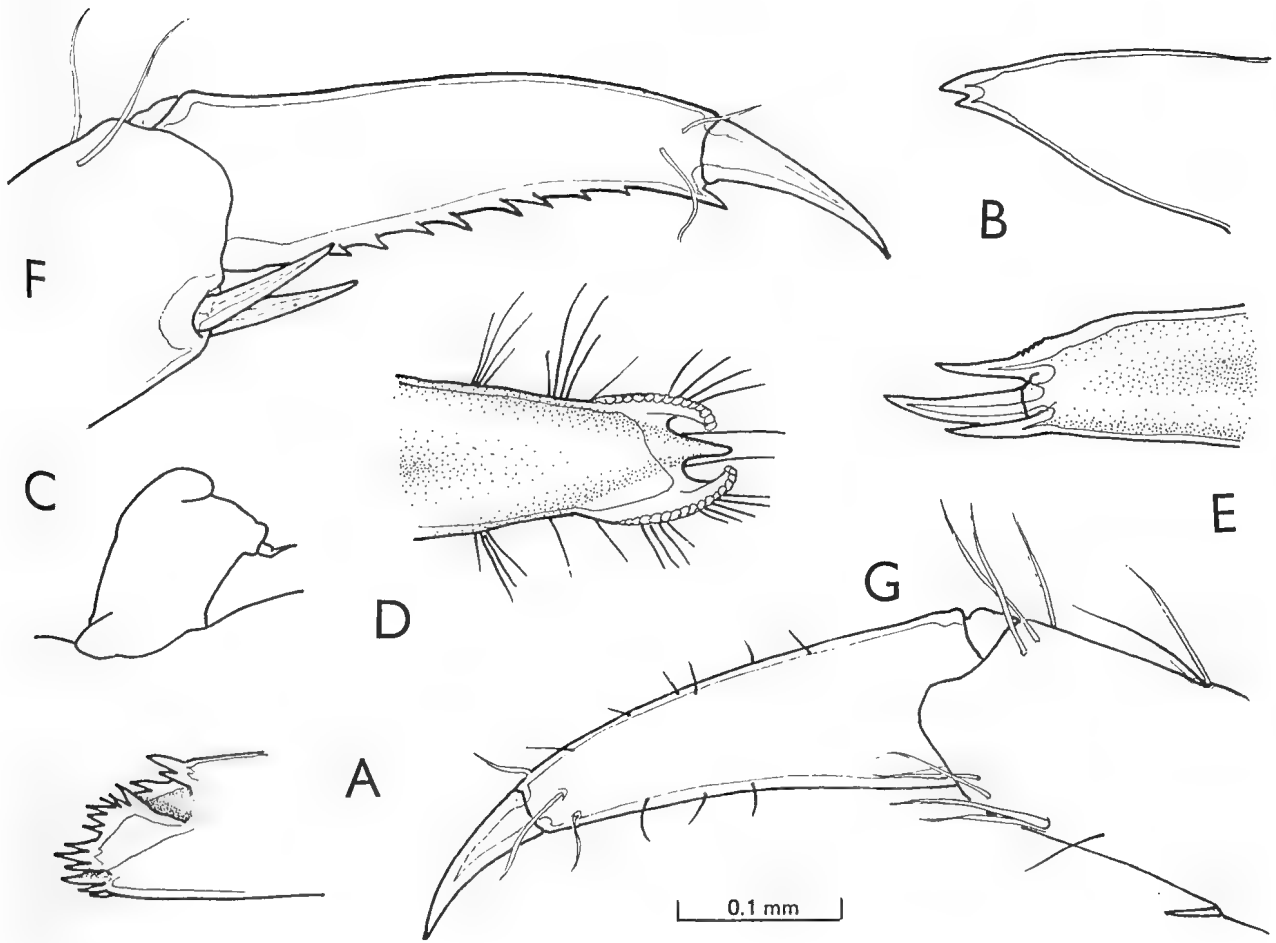


Fig. 6. *Epipontonia anceps* n. sp. A, major second pereiopod. B, chela of major second pereiopod, medial aspect. C, same, fingers, medial aspect. D, same, lateral aspect. E, chela of minor second pereiopod. F, same, fingers, lateral aspect. G, chela of minor second pereiopod. B-F, holotype; A, G, paratypes.

The fourth thoracic sternite is unarmed, and the following sternites are narrow.

The first pereiopods are slender, exceeding the distal end of the antennular peduncle by the distal fourth of the merus. The chela has the palm subcylindrical, slightly compressed, uniform, about 3.0 times longer than deep, with a few cleaning setae proximally. The fingers are slender, equal to about 0.6 of the palm length. The dactylus is narrow, about 3.5 times longer than deep with a small hooked tooth distally, flanked by expansions of the cutting edges which are denticulate and only present over the distal fourth, both medially and laterally, and separated by deep notches. The fixed finger is also slender and tapering, ending in central spine flanked by two shorter teeth, of which one is finely ribbed proximally on the cutting side. The carpus is about 1.5 times the length of the chela, tapered proximally and about 6.5 times longer than its distal width. The merus is slightly longer than the carpus, about 7.5 times longer than its central width. The ischium, basis and coxa present no special features. The coxa is without a median ventral process.

The second pereiopods are well developed, with large, robust, unequal chelae. The major chela has the palm oval in section, tapering slightly distally, finely tuberculate, about 1.7 times longer than the greatest depth, equal to about 1.2 of the post-orbital carapace length. The fingers are compressed, tapering, equal to 1.8–2.0 of the palm length. The dactylus has a stout strongly hooked tip, about 3.1 times longer than deep, with a feebly convex cutting edge, entire except for a small rounded tooth proximally. The fixed finger is tapering, distally acute but less strongly hooked than the dactylus, with the cutting edge entire, concave and grooved proximally, and with a small rounded knob on the proximal lateral aspect of the groove. The carpus is short and stout, equal to a little less than half the length of the palm, about 1.7 times longer than the maximum width, non-tuberculate and distally unarmed. The merus is slightly longer than the carpus, about 0.45 of the palm length, 2.2 times longer than deep, with a blunt disto-ventral angle and sparsely provided with acute tubercles ventrally. The ischium is about 0.8 of the meral length, 2.2 times longer than wide and tapered

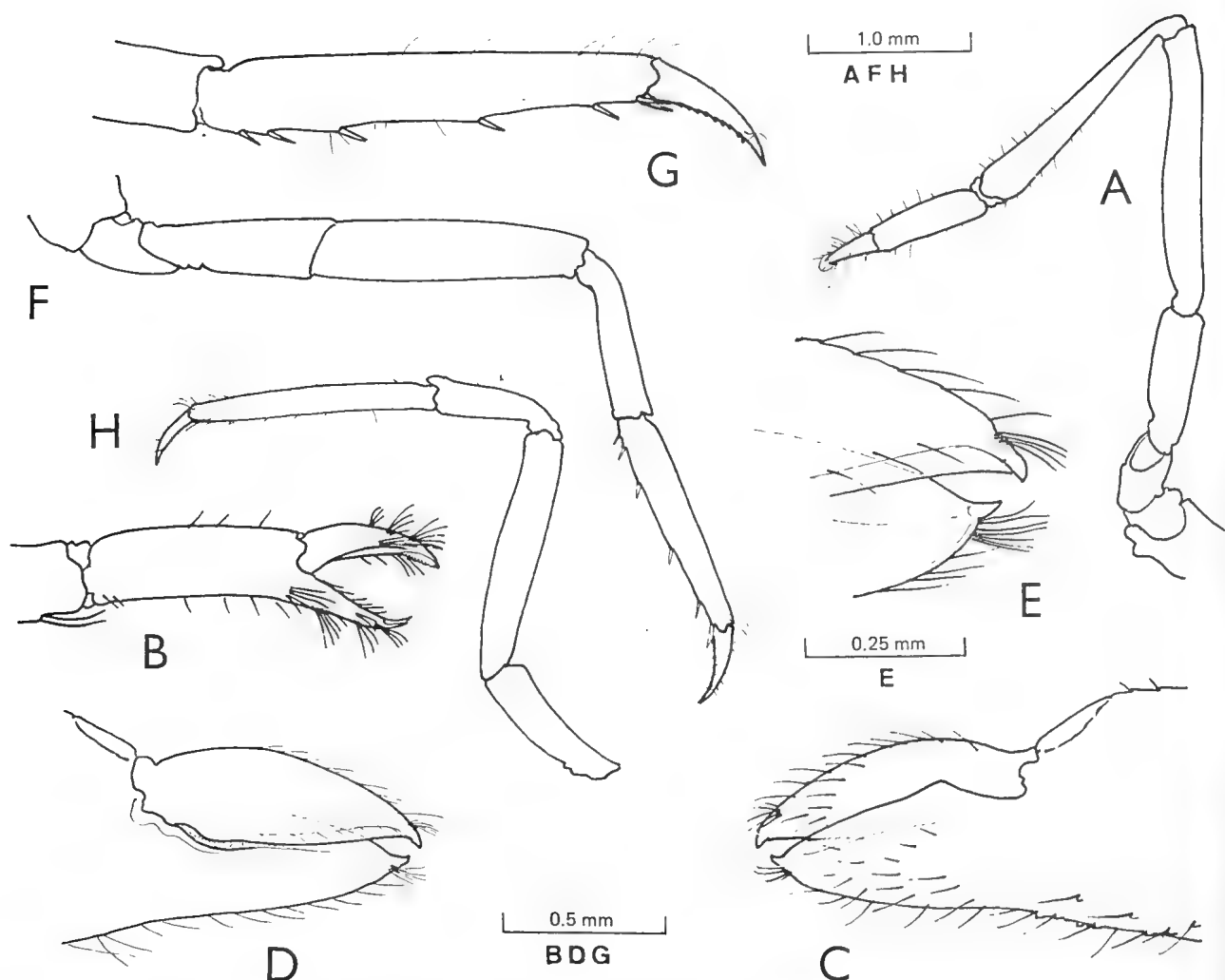


Fig. 7. *Epipontonia anceps* n. sp. Ovigerous female paratype. A, first pereiopod. B, chela of first pereiopod. C, fingers of minor second pereiopod, medial. D, same, lateral. E, finger tips of same. F, third pereiopod. G, propod and dactyl of third pereiopod. H, fifth pereiopod.

proximally. The basis and coxa are robust, without special features. The minor second pereiopod has the chela equal to about 0.6 of the length of the major chela. The palm of the chela is oval in section, feebly tapering distally, finely tuberculate, about 1.8 times longer than deep and equal to about 0.75 of the post-orbital carapace length. The fingers are compressed and tapering, with acute feebly-hooked tips, equal to about 0.7 of the palm length. The dactylus is about 3.0 times longer than deep, with the cutting edge mainly straight, unarmed, with a feeble blunt tooth proximally. The fixed finger is grooved through most of its length, with the medial border of the groove more strongly developed than the lateral and with a small rounded knob proximally. The carpus, merus and ischium are similar to those of the major chela but less robust.

The smallest ovigerous female bears only the minor chela, which differs slightly from the above description. The palm is about 1.85 times longer than wide, with the greatest width centrally rather than proximally, and with the fingers equal to about 0.6 of the palm length. The

dactylus is 3.0 times longer than deep, with the greatest depth at half the length rather than proximally, with the tip less robust and feebly hooked and the cutting edge deeply channelled with the medial border broadly expanded to form a shearing blade working in opposition to the cutting edge of the dactyl. The fingers are also more abundantly provided with long setae than in the other ovigerous female.

The juvenile female has both second pereiopods. The larger chela has the palm stout, about 1.6 times longer than deep, widest at about one third of its length and tapering moderately distally. The dactyl is about 2.6 times longer than deep, with a strongly hooked tip and a sinuous cutting edge with an acute tooth proximally. The fixed finger is very short and deep, with its length about 0.9 of its basal width. The cutting edge is grooved proximally with the ventral lip strongly concave and the dorsal distinct only proximally with an acute tooth. The minor chela is about 0.55 of the length of the major chela and resembles that of the female described above, with the fingers closing with a shearing action.

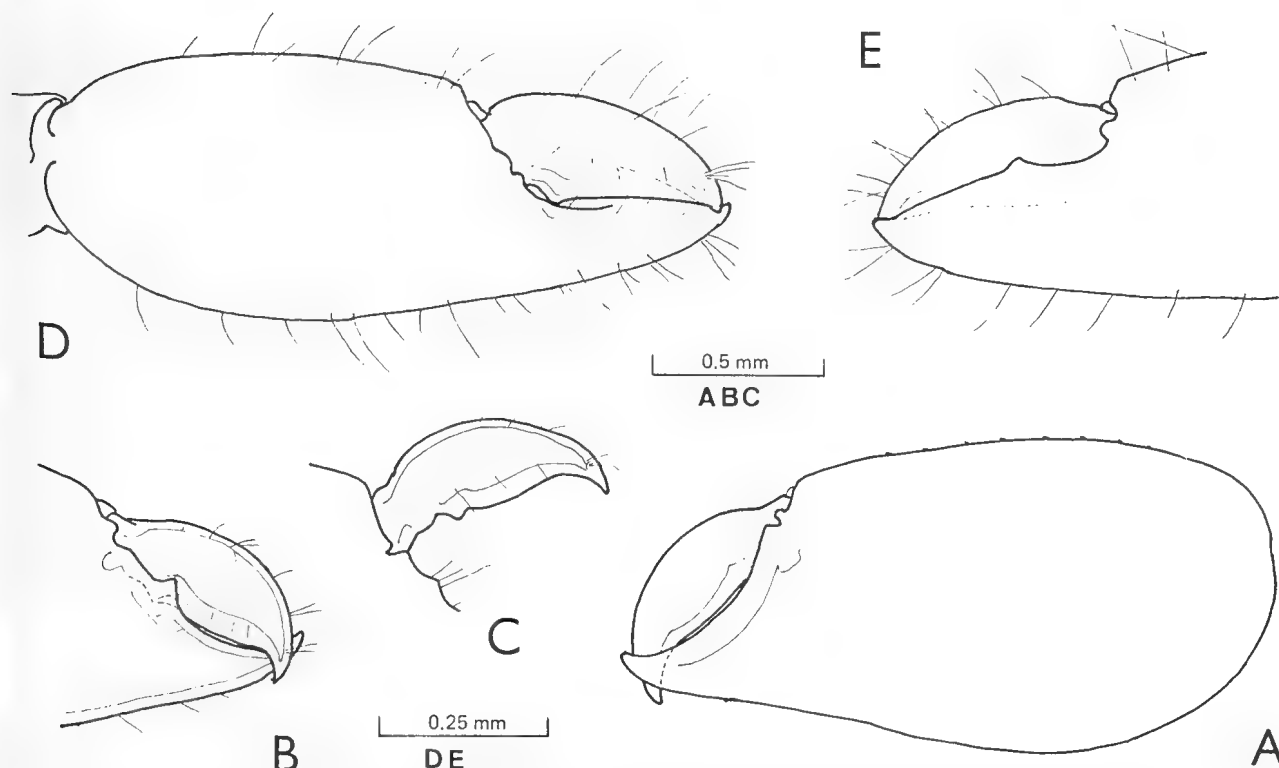


Fig. 8. *Epipontonia anceps* n. sp. Juvenile female. A, chela of major second pereiopod. B, fingers of same, medial aspect. C, dactylus of same. D, chela of minor second pereiopod. E, fingers of same, medial aspect.

The ambulatory pereiopods are slender. The third pereiopod extends anteriorly to exceed the carpocerite by the length of the propod and dactyl. The dactyl is slender, tapering, about 4.5 times longer than deep. The unguis is distinct, simple, acute, about 0.38 of the corpus length and 3.3 times longer than wide. The corpus is 3.4 times longer than wide with an acute disto-ventral accessory tooth and a series of 8 similar but slightly smaller spines distributed along the ventral border. The propod is 3.0 times the length of the dactyl, about 6.3 times longer than deep, tapering slightly distally with a pair of disto-ventral spines and five ventral spines. The carpus is 0.75 of the length of the propod, about 5.0 times longer than wide, uniform and unarmed. The merus is about 1.2 times the propod length, 4.5 times longer than deep, slightly tapered distally and unarmed. The ischium is about 0.85 of the propod length, broadening distally, unarmed and about 3.0 times longer than the distal width. The basis and coxa are normal. The fourth and fifth pereiopods are similar but progressively more slender. The dactylus of the fourth pereiopod has a small distal accessory spine on the corpus but the ventral border is devoid of denticles. The propod has a pair of disto-ventral spines and 1-2 ventral spines only. The fifth pereiopod has the dactylus simple. The propod is slightly longer than that of the third pereiopod, but only 9 times longer than wide, with a single disto-ventral spine only.

The protopodite of the uropod is short and laterally unarmed. The exopod has a convex lateral margin, unarmed but terminating distally in a small acute tooth,

with a large mobile spine situated rather remotely medially. The distal lamina is short, not exceeding the tip of the spine and the length is about 2.3 times the width. The endopod is 2.6 times longer than wide, of similar width to the exopod but distinctly longer.

The ova are numerous and small.

Coloration. Mainly transparent, with a dorsal white stripe outlined by red on the eyestalk. The ophthalmic somite and epistomal region to the first thoracic sternite, the coxa and basis of the first pereiopod and the cutting edges of the fingers of the second pereiopods are all white. The ovary is a translucent white, the stomach rusty red and the hepatopancreas purple.

Host. *Dysidea* sp. (Porifera).

Associated fauna. Four specimens of the alpheid shrimp *Synalpheus neomeris* (De Man) and a single example of the pontoniine shrimp *Typton wasini* Bruce were found on the same host sponge.

The Systematic Position of *Epipontonia anceps*

The genus *Epipontonia* contains only one other species, *E. spongicola* Bruce, 1977, which is closely related to the present species. *E. anceps* may be distinguished from *E. spongicola* by two morphological characteristics in particular: (i) the absence of any antennal spine, and (ii) the presence of three terminal spines on the fixed finger of the chela of the first pereiopod and the expanded, serrated cutting edges, extending forwards on either side of the terminal tooth

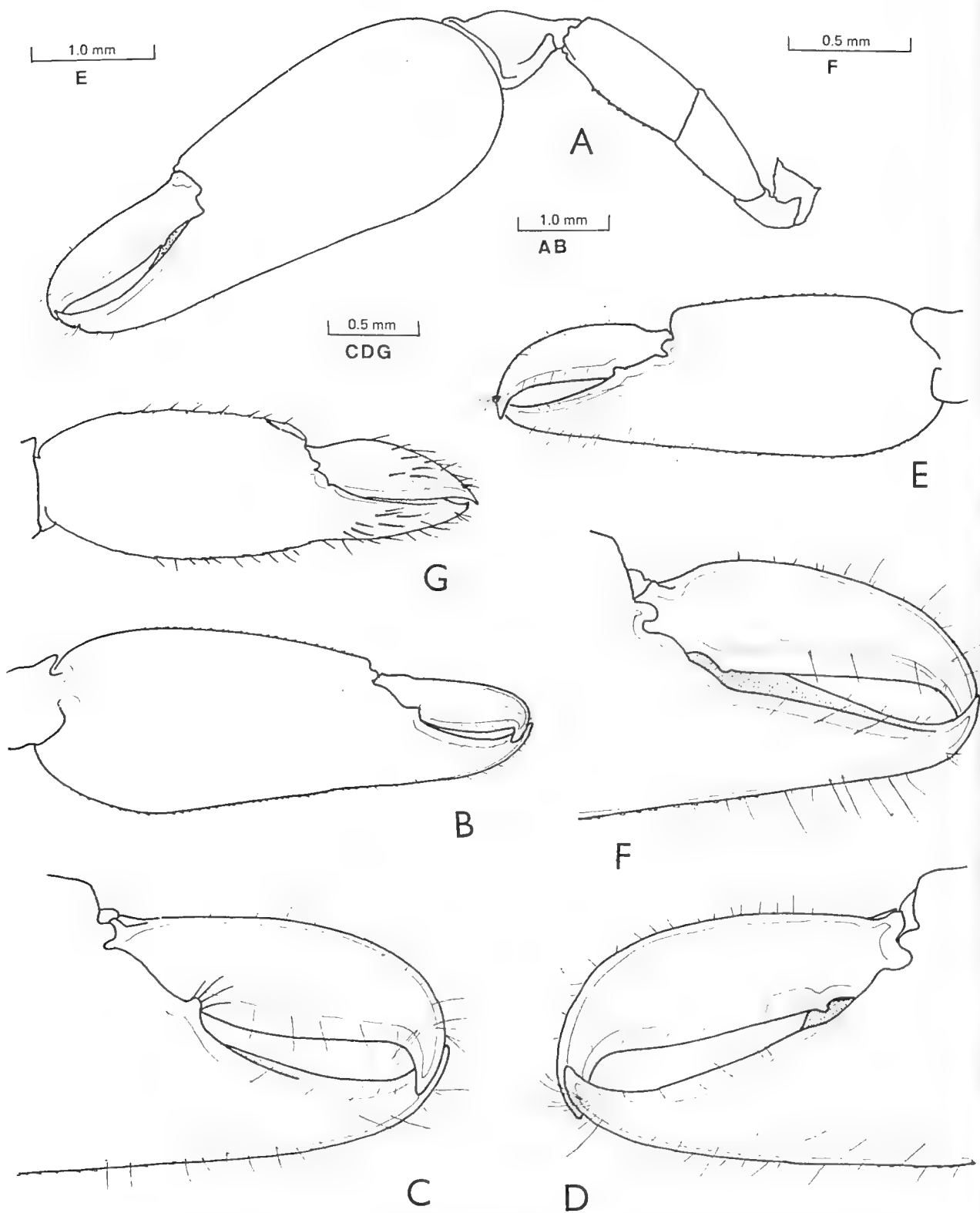


Fig. 9. *Epipontonia anceps* n. sp. Ovigerous female paratype. A, molar process of mandible. B, incisor process. C, palp of maxillula. D, tip of dactyl of first pereiopod. E, tip of fixed finger of first pereiopod. F, dactyl of third pereiopod. G, dactyl of fifth pereiopod.

on the dactylus. Other differences are that the rostral dentition is 6-7/1 compared with 9/1; that the second pereiopods are large and unequal, rather than small and

subequal, and that the corpus of the dactyl of the third pereiopod is denticulate throughout its length, instead of only along the proximal half.

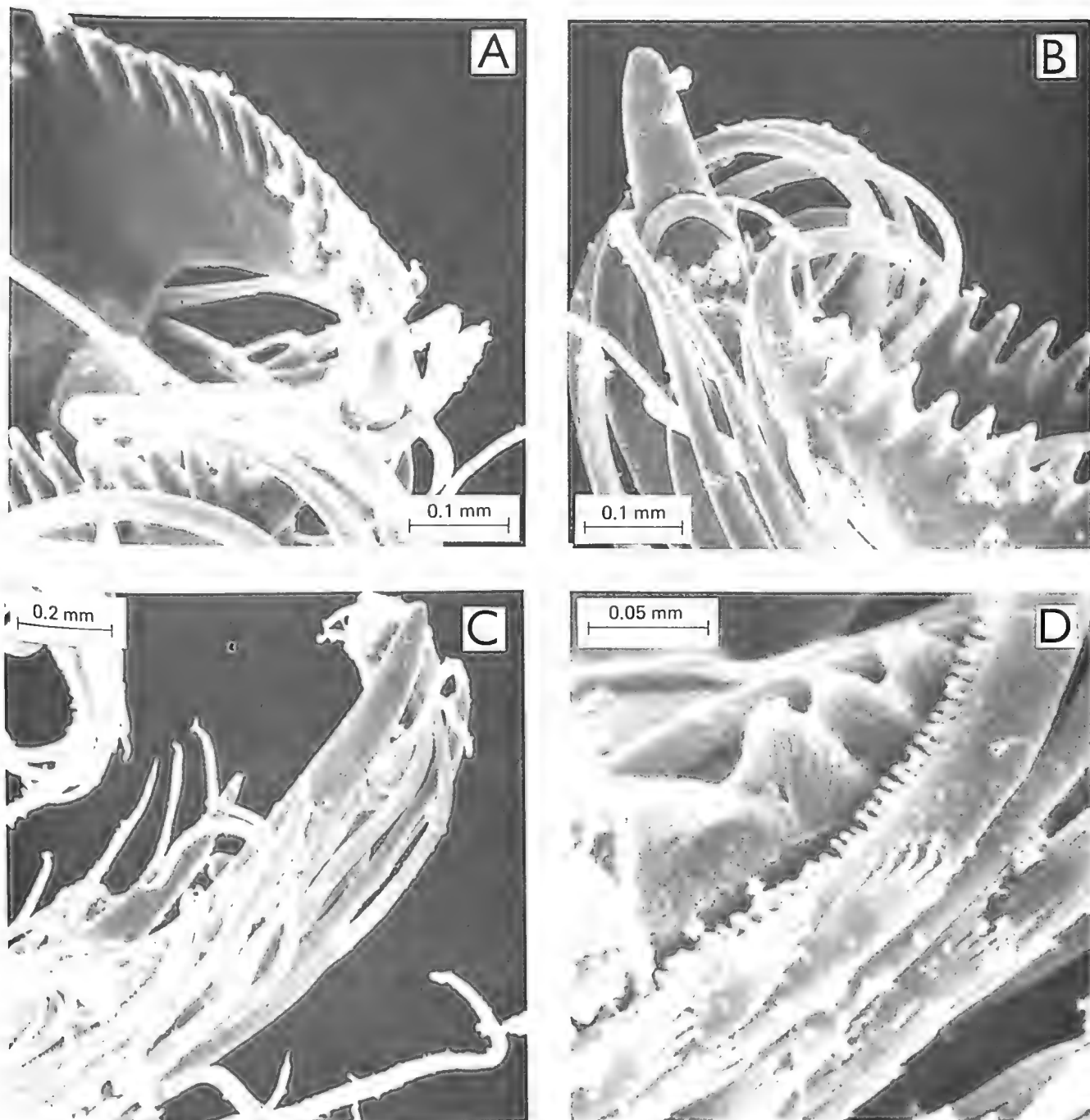


Fig. 10. *Epipontonia anceps* n. sp., paratype female. A, tip of dactyl of first pereiopods, view from the occlusal aspect, showing the strongly dentate lateral expansions, separated by a deep notch from the stout hooked terminal tooth. B, same, oblique lateral aspect. C, tip of fixed finger of chela of first pereiopod, showing slender accessory teeth adjacent to the slender, feebly-curved distal tooth. D, same, detail of small denticles on the base of the accessory spine, and the adjacent setae, showing pectinate inner border with palmate scales laterally.

Discussion

The single known example of *Epipontonia spongicola*, from Wasin Island, Kenya, was found in association with a sponge of the genus *Reniera* (Demospongia, Monaxonida). The present specimens of *E. anceps* were found in association with a sponge of a different subclass, of the genus *Dysidea* (Demospongia, Keratosa). Sponges of the genus

Dysidea have also been found to host three other pontoniine shrimps, *Typton wasini* Bruce, *Periclimenaeus bidentatus* Bruce and *P. rastrifer* Bruce.

The homology of the spine present over the lateral aspect of the orbit in *E. anceps* presents some difficulty in interpretation, as also occurs in the cases of several other pontoniine shrimps. The small spine present approximately over the upper edge of the basicerite in *E. spongicola* is considered to represent an antennal

spine and the larger spine situated at a more dorsal position at the level of the basiophthalmite, in both *E. spongicola* and *E. anceps*, is treated as a para-orbital spine, and homologous with the spines found in this situation in many of the species of the genus *Typton* Costa. A similar spine is also present in some species of *Onycocaris* Nobili, e.g. *O. longirostris*, but is absent in others such as *O. amakusensis* and *O. callyspongiae* (Bruce, 1980; Fujino & Miyake, 1969).

The occurrence of large and unequal chelae on the second pereopods in *E. anceps*, in contrast to the small and subequal chelae in *E. spongicola*, increases the resemblance of the genus to *Periclimenaeus* Borradaile but the present specimens are primarily distinguishable from species of that genus by the absence of a sound producing pit and hammer mechanism on the fingers of the major chela. The fingers of the minor chela do not generally oppose with a shearing action in *Periclimenaeus* and the second maxilliped is also

provided with a normally-developed epipod (Holthuis, 1952), which is absent in both species of *Epipontonia*.

ACKNOWLEDGEMENT. I am indebted to Dr J. Vacelet for the identification of the sponge host.

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The Australian Scincid Lizard Genus *Calyptotis* De Vis:
Resurrection of the Name, Description of Four New Species,
and Discussion of Relationships

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ABSTRACT. Five species of small cryptozoic skinks from the woodlands and forests of eastern Australia are diagnosed as a monophyletic group and given generic rank. The name *Calyptotis* De Vis 1886 is resurrected from the synonymy of *Sphenomorphus* for the genus. Four of the species are described as new and the one previously described species—*C. scutirostrum* W. Peters 1873—is reviewed. Information is provided on distribution, ecology and reproduction for each species. The interspecific and intergeneric relationships of *Calyptotis* are discussed. A key to the species is provided.

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Abbreviations and Symbols

AM:	Australian Museum	NMV:	National Museum of Victoria
BMNH:	British Museum (Natural History)	QM:	Queensland Museum
CAS:	California Academy of Sciences	QNP:	Queensland National Parks and Wildlife collections
MVZ:	Museum of Vertebrate Zoology, University of California, Berkeley	SAM:	South Australian Museum
		SD:	standard deviation
		SVL:	snout–vent length

WAM: Western Australian Museum

\bar{X} : statistical mean

ZMB: Zoologisches Museum, Berlin

*, **,

***: the .05, .01 and .001 levels of significance for statistical tests

The *Sphenomorphus* group is a major lineage of lygosomine skinks that comprises approximately 16 genera and 385 species. It ranges from south-eastern Europe and southern Asia east through the Indo-Australian Archipelago to the Solomon Islands and south into Australia; representatives of the group also occur in south-eastern North America and Middle America. The genera currently recognized in this group are *Ablepharus*, *Anomalopus*, *Ateuchosaurus*, *Ctenotus*, *Eremiascincus*, *Hemiergis*, *Isopachys*, *Lerista*, *Lipinia*, *Lobulia*, *Notoscincus*, *Prasinohaema*, *Saiphos*, *Scincella*, *Sphenomorphus* and *Tropidophorus* (Greer, 1979).

Most of these genera represent monophyletic groups with well-defined morphologies and ecologies. The outstanding exception, however, is *Sphenomorphus*, a widely distributed group of approximately 180 species allied primarily on the basis of primitive traits and including animals as different as long-legged, diurnal climbers and reduced-limbed, cryptozoic burrowers. Several lineages are evident within *Sphenomorphus* but their formal taxonomic recognition is handicapped by a bewildering amount of variation, some of which is due to tight morphoclines among closely related species and some to convergence between distantly related species.

Recent work on *Sphenomorphus* has shown that there is a group of five species in eastern Australia that appears to be quite distinct within the *Sphenomorphus* group as a whole and which can be reasonably assigned to a separate genus. One purpose of this paper is to diagnose this taxon and to resurrect the name *Calyptotis* De Vis for it. Of the five species referable to *Calyptotis*, one only—*C. scutirostrum*—has been described, and it remains poorly known. A second purpose of this paper, therefore, is to describe the remaining four and review the one named species and to give details of the biology of all five. Finally, many of the characters that distinguish the species of *Calyptotis* both individually and as a group are amenable to phylogenetic analysis and hence provide a basis for inferring the intra- and intergeneric relationships of the group. A third purpose of this paper is to develop this analysis and to discuss some of its implications.

Resurrection of the Genus *Calyptotis* De Vis

The five eastern Australian species to be discussed here—*Sphenomorphus scutirostrum* and its four undescribed relatives—appear to be unique in the *Sphenomorphus* group (Greer, 1979) in possessing the following combination of derived character states (see Appendix for character analysis): palatal rami of

pterygoids roughly triangular in shape (narrow anteriorly and broad posteriorly) and separated to varying degrees by posteriorly extending processes from posteromedial corners (Fig. 21); phalanges in fourth toe of manus four; postmental in contact with only one infralabial; loreal single; and fourth supralabial subocular (Figs 2, 5, 8, 11, 13). The five species also share the following more difficult-to-interpret features: small size (maximum SVL 59 mm or less); low number of longitudinal scale rows at midbody (19–24); and bright coral pink to red colour on the ventral surfaces of the posterior part of the body and the tail (in at least four of the five species).

As it is construed here the group occurs disjunctly on Thornton Peak in north-eastern Queensland and then more or less continuously from the Clarke Range in central-eastern Queensland south to the area just north of the lower Hunter River Valley in central-eastern New South Wales (Fig. 14). Within this area the group is confined to the woodlands and forests of the coastal plain and adjacent highlands. Nowhere does it occur more than 170 kilometres inland.

The species in the group have the ecological distinction of being one of the most abundant lizards in the habitats they occupy, especially in the southern part of the distribution. The animals are cryptozoic but may be readily collected by turning over logs and rocks and quickly pouncing on uncovered individuals before they wriggle into the leaf litter and loose soil. In size, microhabitat and escape behaviour they are very similar to the terrestrial, woodland salamanders of the genus *Plethodon* in North America.

The morphological and ecological similarity of these species plus their more or less contiguous distribution suggests that they are a monophyletic group. Furthermore, I think the morphology of the group is distinctive enough to accord it separate generic rank and hence propose that the name *Calyptotis* De Vis 1886 (type species, by monotypy: *Calyptotis flaviventer* De Vis = *Lygosoma scutirostrum* Peters) be resurrected from the synonymy of *Sphenomorphus* for it.

In the following section I review the one previously described species—*C. scutirostrum*—and describe the four new species: *C. ruficauda*, *C. lepidorostrum*, *C. temporalis* and *C. thorntonensis*. The species are discussed roughly in the order of their increasing number of derived character states.

THE SPECIES OF *CALYPTOTIS*

Calyptotis ruficauda n.sp.

Figs 1, 2

Holotype. Australian Museum R 52338; Portion 14, Parish of Dingle, Shire of Bellingen, N.S.W. Altitude c.165 m. Collected by H.G. Cogger. The type locality is just west of Brinerville which is approximately 50.5 km W of Bellingen Post Office by the road through Thora. The coordinates of the type locality are 152°33'E, 30°28'S.

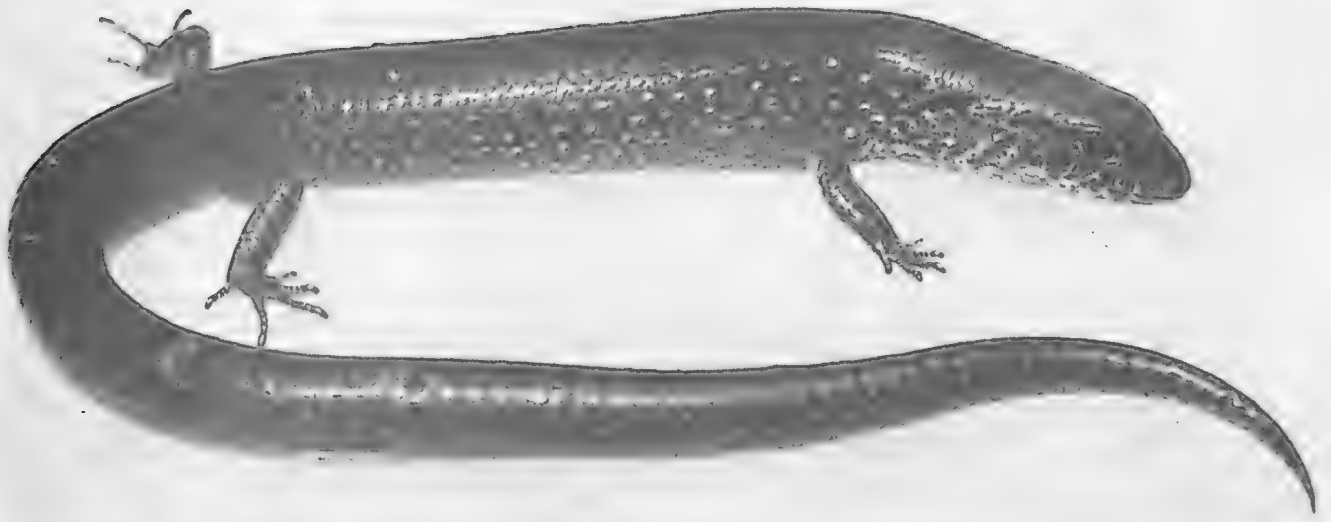


Fig. 1. *Calyptotis ruficauda* (AM R 62876) from the vicinity of Brinerville, NSW.

Paratypes. All localities are in New South Wales.

American Museum of Natural History 120298–303: Same locality data as holotype; 120304–5: 10 km SSW of Macksville via Hwy 1.

Australian Museum R 4804: Manning River; R 6283: Gurravambi, near Macksville on the Nambucca River; R 15526–15529: Boolambayte; R 16024: Laurieton; R 18650, 18653: Middle Brother Mountain; R 20522–20531, 26011, 27732: Bulahdelah; R 35186: between Five Day and Branch Creeks, near Comara; R 38216, 38267, 38269, 38300–38303, 52339–52343, 54600–54601, 57531–57532, 61173–61195, 62876–62877, 71429–71432: Portion 14, Parish of Dingle, Shire of Bellingen; R 53164–53165: junction of Pacific and Oxley Highways; R 53166–53167: ranges W of Wingham; R 54749–54750, 90316–90330: 1.7 km W of Pacific Highway via road to lookout on Middle Brother Mountain; R 57845–57850: 11 mi S of Coffs Harbour; R 61205–61208: 12.0 km W of Wauchope Post Office via road to Bellangry; R 60387–60389: Wallingat State Forest near Forster; R 66590: Cape Hawke new Forster; R 66623–66627: Park Beach, Coffs Harbour; R 66628: Moonee Beach; R 68477–68481, 75971: Rochester Fire Trail, 5 km N of Nahi; R 69541–69551: approximately 0.5 km W of Pacific Highway along Louise's Ridge Road, just S of Warrel Creek; R 70317, 84993–84995: Sea Acres Fauna Sanctuary, Port Macquarie; R 71237: just S of Barrington Guest House, Chichester State Forest; R 90607–90608: Black Scrub Track, Bellinger River State Forest; R 92305: Bellbrook; R 92912: compartment 134, Middle Brother State Forest.

Northern Territory Museum: R 4697–4703: Dongdingalong Estate, Burnt Ridge Road, South Kempsey.

Queensland Museum: J 26024: O'Sullivan Gap.

Diagnosis. *Calyptotis ruficauda* differs from its congeners in possessing prefrontal scales and a well-developed external ear opening with a scaleless tympanum.

Description. *Calyptotis ruficauda* is a medium-sized (maximum SVL = 55 mm) light to dark brown skink with nonoverlapping, pentadactyl limbs and a rather

uneven dark brown dorsolateral streak that is most distinct on the head and neck (Fig. 1).

Snout moderately short and deep; rostral projecting slightly between nasals; frontonasal wider than long; prefrontals present, well developed but almost invariably separated medially; frontal considerably longer than wide, shorter than midline length of frontoparietals and interparietal; supraoculars four, anterior two (or rarely three) in contact with frontal; frontoparietals distinct, each equal to or slightly larger than interparietal in total area; interparietal distinct, with small clear parietal eye spot posteriorly; parietals in broad contact behind interparietal; each parietal bordered posterolaterally by upper secondary temporal, anteriormost nuchal (which is always transversely enlarged) and usually a slightly smaller scale intercalated between the two.

Nasal moderate in size, widely separated from its fellow, with nostril centrally located; loreal single, equal to or slightly larger than nasal; preoculars two; supraciliaries six to eight (mode = seven), first and last largest; postoculars two; subocular series complete, comprising five scales, third of which is small and partly in eyelid; lower eyelid scaly; supralabials six, fourth below centre of eye; primary temporal single; secondary temporals two, dorsal much larger than ventral, which is about equal in size to primary temporal; external ear opening large, more or less vertically oval; tympanum slightly recessed, scaleless, only slightly pigmented if at all; infralabials four, first only in contact with postmental; mental followed by postmental and a pair of chin scales in medial contact (Fig. 2).

Transversely enlarged nuchals 1–4 (\bar{X} = 2.5, mode = 2) on each side; body scales smooth, in 20–24 (\bar{X} = 22.1, mode = 22) longitudinal rows at midbody; scales in paravertebral rows slightly to moderately wider than scales in more lateral rows, 51–59 (\bar{X} = 53.9) in

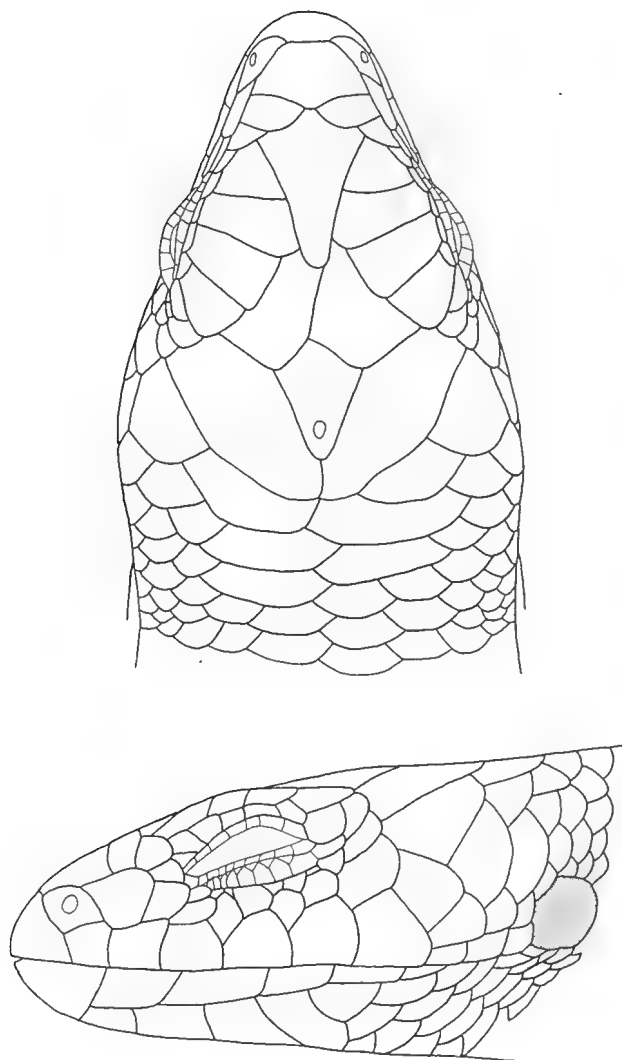


Fig. 2. Dorsal and lateral views of the head of *Calyptotis ruficauda* (AM R 90329) from Middle Brother Mountain, NSW.

a single row¹; medial pair of preanals greatly enlarged; each preanal overlaps the preanal lateral to it and is in turn overlapped by the preanal medial to it; medial row of subcaudals slightly wider than more lateral rows.

Digits moderate in length; fourth toe slightly to appreciably longer than third, covered by two longitudinal rows of scales for most of length (except for two most-distal scales which are single); subdigital lamellae on fourth toe with keels that begin as rounded tubercles basally, become obtuse ridges over middle length and are lost distally, 10–15 (\bar{X} = 12.8, mode = 13).

Snout-vent length 21–53 mm; tail length 1.13–1.53 times SVL; front leg .17–.25 and rear leg .24–.33 times SVL.

¹The paravertebral scales are counted from the first scale that falls behind an imaginary line connecting the back side of the thighs, when they are held perpendicular to the long axis of the body, forward to and including the anteriormost nuchal.

Presacral vertebrae 26; phalangeal formulae for manus and pes 2–3–4–4–3 and 2–3–4–5–3 respectively.

Colour in preservative. The dorsum is light to medium dark brown usually with darker brown flecks on the head and dark brown spots aligned linearly through the centres of the four dorsalmost scale rows. These dorsal spots are generally strongest and most likely to be coalesced into continuous stripes on the nape and anterior part of the body. In some specimens, however, the dark dorsal spots are totally lacking.

An uneven but usually distinct dark brown dorsolateral streak begins just before the eye and passes posteriorly onto the body. This streak is generally most distinct on the head, neck and anterior part of the body.

The flanks are light brown to grey with scattered dark brown spots which are usually larger and more coalesced than the dorsal body spots. The lateral dark spots are most distinct on the neck and often grade into the diffuse lower edge of the dark dorsolateral streak, especially on the mid and posterior parts of the body. Diffuse light spots are scattered over the flanks and are generally most distinct in the dark dorsolateral streak and the darker upper areas of the flanks. Dark pigment edges the labial scales (Fig. 1).

There is often dark spotting on the chin, throat and anterior part of the chest, but there was no sexual dimorphism in the intensity of the spotting (X^2 = .11 NS, N = 54). There is often fairly even fine spotting on the underside of the tail, but the intensity of this spotting, as judged on the base of the tail where it is most variable, also showed no sexual dimorphism (X^2 = .16 NS, N = 52).

Colour in life. Detailed colour notes were taken on 17 specimens collected on Middle Brother Mountain, NE of Taree, New South Wales on 15 March 1976 and on 23 specimens collected in the vicinity of Brinerville, New South Wales on 20 April 1977. These notes provide the basis for the following assessment of colour in life.

All the Middle Brother Mountain specimens were recorded as having pale yellow colour on the venter of the body from the level of the forelegs back to the pelvic area. The smallest specimen, an unsexed obvious hatchling with an SVL of 21 mm, showed no pink colour anywhere, but all other specimens, which comprised seven females of SVL 34–47 mm and nine males of SVL 34–46 mm, had coral pink colour on the underside of the tail.

Notes on the intensity of the pink tail colour were made for 14 of the 16 specimens with tail colour. This subset comprised six females of SVL 34–45 mm and eight males of SVL 34–46 mm. The single smallest individuals of both sexes in this group, both of 34 mm SVL, were not noted as having intense tail colour. The remaining seven males, which had SVLs of 35 (2), 38, 41, 42, 43 and 46 mm, all had intense tail colour, but of the five remaining females only two, both of 43 mm SVL, had intense colour, whereas three with SVLs of 35, 35 and 45 mm, did not. When tail colour is intense, it extends across the vent and onto the undersides of the thighs.

After 10 months in preservative, only four of the five largest males of the 16 specimens with any tail colour in life retained any trace of this colour.

The four smallest specimens (SVL 23–27 mm) of the 23 collected in the Brinerville area on 20 April lacked all ventral colours. The remaining 19 specimens (11 females of SVL 31–53 mm and eight males of SVL 38–55 mm) were a pale yellow colour on the underside of the body and pink on the underside of the tail. Of these, the two smallest males (SVL 38 and 42 mm), the five smallest (SVL 31–48 mm) females and two of the remaining females (SVL 51 and 52 mm) had only pale pink tail colour while the five remaining and largest males (SVL 45–55 mm) and four of the six largest females had intense pink tail colour.

These data suggest the following: (1) all but perhaps the youngest individuals have some pink colour on the underside of the tail; (2) the colour tends to be expressed intensely at smaller sizes more often in males than in females; (3) the colour is expressed intensely more often in males than in females in any size class, and (4) the colour is more durable in preservative in males than in females.

Details of holotype. The holotype (AM R 52338) is a male with a snout–vent length of 51 mm and a tail length of 63 mm, of which 24 mm is regenerated; supraciliaries 7/7; enlarged nuchals 2/4; midbody scale rows 22; paravertebrals 53, and subdigital lamellae 13/13.

Etymology. The name *ruficauda* is intended to call attention to the coral pink underside of the tail in many of the larger individuals of the species.

Size. There is some indication in the large series from Brinerville that males may attain larger size than females. Thirty-nine of the 46 animals from this locality can be sexed and measured accurately and the largest of the 21 males is 55 mm SVL while the largest of the 18 females is only 53 mm.

Distribution. *Calyptotis ruficauda* is restricted to the lowlands of the central north coast of New South Wales in the area between Brinerville and Moonee Beach in the north and Barrington Guest House and Bulahdelah in the south (Figs 3 and 14).

Calyptotis ruficauda is the most southern of the five species of *Calyptotis*. Its nearest neighbour is *C. scutirostrum*. The two species are separated by the Dorrigo Plateau, an eastern spur of the Dividing Range. *C. ruficauda* occurs in the Bellinger River Valley on the south side of the Plateau and on the coastal plain just to the east, and *C. scutirostrum* occurs on the north-western slopes of the Plateau. In the south *C. ruficauda* reaches the limit of its range in the foothills of the Dividing Range on the north side of the Hunter River Valley and in the adjacent coastal plain.

Habitat. Information on the habitat associations of *C. ruficauda* are most complete for two areas: Middle Brother Mountain and Brinerville. At Middle Brother Mountain the species was found abundantly under logs in fairly open, but moist, sclerophyll forest both on flat areas and on the sides of fairly steep slopes. Other species collected in the same habitat at the same time were *Pseudophryne coriacea* and *Lampropholis delicata*.

In the Brinerville area the species is found under rocks and logs in habitats ranging from the edge of rainforest to fairly open dry sclerophyll forest—but always in moist microhabitats.

These plus other more incidental observations suggest that *C. ruficauda* occurs largely in the moister parts of both dry and wet sclerophyll forest and at the edge of rainforest. There appear to be no records from the interior of moist rainforest but this habitat is only poorly represented within the range of *C. ruficauda*. The species does, however, occur in seasonably dry coastal vine thickets, e.g., Sea Acres Fauna Sanctuary.

Reproduction. There are ten gravid females in the available sample: four contain ovarian eggs and were collected in the period 5 September–17 December in various years and the remainder contain oviducal eggs and were collected in the period 10 November–12 January (Table 1). The oviducal eggs are surrounded by a thick shell, which suggests that the species is oviparous. The mean SVL of the gravid females is 48.5 mm and their mean clutch size is 3.3. There is a significant positive correlation between the SVL of the females and their clutch size ($r = .79^{**}$, $N = 10$).

Table 1. Summary of information on the gravid specimens of *Calyptotis ruficauda*. The superscript “o” indicates enlarged ovarian eggs (in contrast to oviducal eggs) and the letters “R” and “L” indicate right and left ovaries or oviducts, respectively. All localities are in New South Wales.

Specimen	Locality	Date	SVL (mm)	Brood Size
AM R 53167	W of Wingham	?	51	1R-3L = 4 ^o
AM R 54600	Brinerville	5 Sept 1972	52	3R-1L = 4 ^o
AM R 60387	Wallingat State Forest	10 Nov 1977	48	1R-2L = 3 ^o
AM R 69542	Just S of Warrel Ck.	17 Dec 1977	48	1R-1L = 2 ^o
AM R 60388	Wallingat State Forest	10 Nov 1977	52	4R-2L = 6
AM R 69541	Just S of Warrel Ck.	17 Dec 1977	48	2R-1L = 3
AM R 69543	Just S of Warrel Ck.	17 Dec 1977	47	2R-1L = 3
AM R 69546	Just S of Warrel Ck.	17 Dec 1977	47	1R-1L = 2
AM R 57849	11 mi S of Coffs Harbour	27 Dec 1940	42	1R-1L = 2
AM R 66625	Coffs Harbour	12 Jan 1969	50	2R-2L = 4

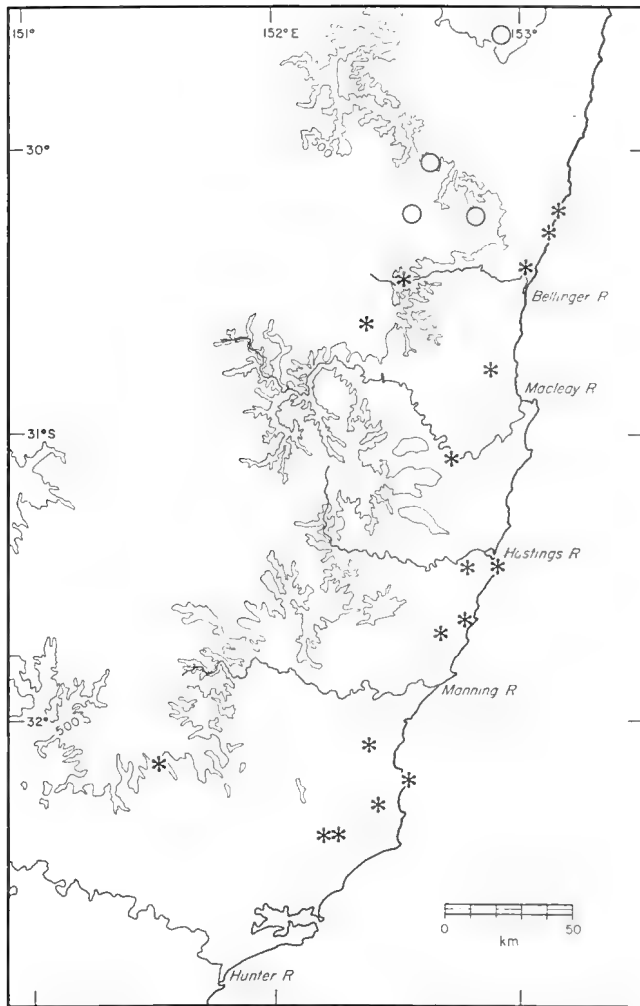


Fig. 3. Map of the north-central coast of New South Wales showing the distribution of *Calyptotis ruficauda* (asterisks) and the extreme southern part of the distribution of *C. scutirostrum* (open circles). The contour line is 500 m.

A large series of *C. ruficauda* from the vicinity of Brinerville, collected on 20 April 1977, contains eight females as large as or larger than the smallest known gravid *C. ruficauda* (SVL = 42 mm). As none of these specimens is gravid, it is probable that the females in this population were reproductively quiescent at the time of collection.

Sex ratio. The population in the vicinity of Brinerville, N.S.W. has been collected more thoroughly than any other and thus provides the best insight into sex ratios in the species. Of the 39 specimens collected from this population, 33 can be accurately sexed, and of these 17 are males and 16 females, a ratio not significantly different from 1:1.

Comparison with other *Calyptotis*. *Calyptotis ruficauda* differs from *C. lepidorostrum* in having the external ear represented by a moderately recessed, naked tympanum instead of a scaly, conical depression; more midbody scale rows (20–24, \bar{X} = 22.1, N = 59 vs 20–24, \bar{X} = 20.6, N = 87; t = 10.31***); fourth toe appreciably longer than third instead of only slightly longer; more subdigital lamellae on the fourth toe

(10–15, \bar{X} = 12.8, N = 61 vs 8–14, \bar{X} = 11.0, N = 88; t = 9.13***); and fewer presacral vertebrae (26 vs 29).

Calyptotis ruficauda differs from *C. scutirostrum* in having prefrontals present instead of absent; the external ear represented by a recessed, naked tympanum instead of a scaly, conical depression; more midbody scale row (20–24, \bar{X} = 22.1, N = 59 vs 19–24, \bar{X} = 20.7, N = 107; t = 8.95***); fourth toe appreciably longer than third instead of only slightly longer; more subdigital lamellae on the fourth toe (10–15, \bar{X} = 12.8, N = 61 vs 7–13, \bar{X} = 10.0, N = 103; t = 16.13***); and fewer presacral vertebrae (26 vs 29–30).

Calyptotis ruficauda differs from *C. temporalis* in having the posteriorly projecting process from the posteromedial corner of the palatal ramus of the pterygoid short instead of long; prefrontals present instead of absent; secondary temporals two instead of one; tympanum perhaps slightly more deeply recessed; more midbody scale rows (20–24, \bar{X} = 22.1, N = 59 vs 20–22, \bar{X} = 20.6, N = 8; t = 5.82***); fourth toe appreciably longer than third instead of subequal; phalanges in fourth toe of pes five instead of four; more subdigital lamellae on the fourth toe (10–15, \bar{X} = 12.8, N = 61 vs 8–10, \bar{X} = 9.0, N = 8; t = 11.28***); and more paravertebrals (51–59, \bar{X} = 53.9, N = 28 vs 46–50, \bar{X} = 47.8, N = 8).

Calyptotis ruficauda differs from *C. thorntonensis* in having the head and body moderately deep instead of depressed; external ear represented by a recessed, naked tympanum instead of a scaly, discoidal depression (scaly, superficial tympanum); postorbital bone present instead of absent; possibly fewer midbody scale rows (20–24, \bar{X} = 22.1, N = 59 vs 24, N = 5); fourth toe appreciably longer than third instead of subequal; phalanges in fourth toe of manus four instead of three; phalanges in the fourth and fifth toes of pes five and three respectively instead of four and four, and fewer subdigital lamellae (10–15, \bar{X} = 12.8, N = 61 vs 8–10, \bar{X} = 8.8, N = 5).

For a tabular comparison of various meristic mensural and proportional characters in *Calyptotis* see Table 5.

Calyptotis lepidorostrum n.sp.

Figs 4, 5

Holotype. Queensland Museum J 33612: Bulburin State Forest, Queensland. Altitude 540 m. Site No. 1 in the Australian Museum and Queensland Museum's joint faunal survey of the eastern Australian rainforests (Anonymous, 1976 and Broadbent and Clark, 1976), or more approximately c. 8.5 km E of Builyan, Qld. The coordinates of the type locality are 24°31'S, 151°29'E.

Paratypes. All localities are in Queensland.

Australian Museum: R 47511, 47640, 47645, 47676, 47680: Bulburin State Forest; R 59243: 0.5 km E of Mary Cairncross Park, Blackall Range; R 59244: Eungella area; R59245–59246, 76221–76223: 2.5 km S of the main forestry road via the Mt. Gerald–Sunday Creek road, Conondale Range, Jimna State Forest; R 76147: 2.3 km SW of junction of Mosman and



Fig. 4. *Calyptotis lepidorostrum* from Bundaberg, Qld. Photo: H.G. Cogger.

Boyne roads via the Boyne road, Bulburin State Forest; R 76188–76212: vicinity of the forestry camp, Bulburin State Forest; R 91082–91099, 90300–90315: along Poona Lake road, Cooloolo State Forest.

Queensland Museum: J 22067: near forestry airstrip, Ungowa, Fraser Island; J 22274: shores of Coomba Lake, Fraser Island; J 22472–22473, 25397: Cooloolo; J 23810, 24133, 29093, 33610, 33613–33615: Bulburin State Forest; J 33737: forestry camp, Bulburin State Forest; J 33752: Granite Creek, Bulburin State Forest; J 24373: Mackay; J 30229, 30236: Big Tuan Creek via Maryborough; J 30231: near Missings Bridge, Tinana Creek; J 31575: Fraser Island National Park, Fraser Island; J 32653–32655, 32671, 32673, 32707–32716, 32721–32722, 32734–32738: Crediton; J 35309, 35879, 35881–35882: Tuan State Forest via Maryborough; J 35878: Missing's Camp, Tuan State Forest via Maryborough; J 35880: Cooper's Gully, Tuan State Forest. Queensland National Parks and Wildlife Service: 5, 87: Lake Poona, Cooloolo National Park; 11286, 11295: Eungella National Park.

Diagnosis. *Calyptotis lepidorostrum* differs from its congeners in the following combination of characters: prefrontals present instead of absent; external ear represented by a scaly, conical depression instead of a recessed naked tympanum or a shallow, scaly, discoidal depression, and head and body moderately deep instead of depressed.

Description. *Calyptotis lepidorostrum* is a medium sized (maximum SVL = 55 mm) light to dark brown skink with nonoverlapping limbs and a dorsal colour pattern comprising a thin dark brown dorsolateral streak, which is especially well developed on the head, neck and anterior body, and often a line of dark spots or dashes through each of the four dorsalmost scale rows (Fig. 4).

Snout moderately short and deep; rostral projecting slightly between nasals; frontonasal wider than long; prefrontals usually present, rarely in contact (see below); frontal considerably longer than wide, slightly shorter than midline length of frontoparietals and interparietal together; supraoculars four, anterior two in contact with frontal; frontoparietals distinct, each equal to or slightly larger than interparietal in total area; interparietal distinct, with a small clear parietal eye spot posteriorly;

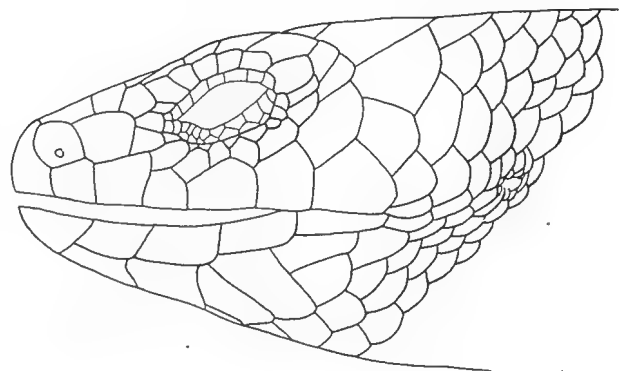
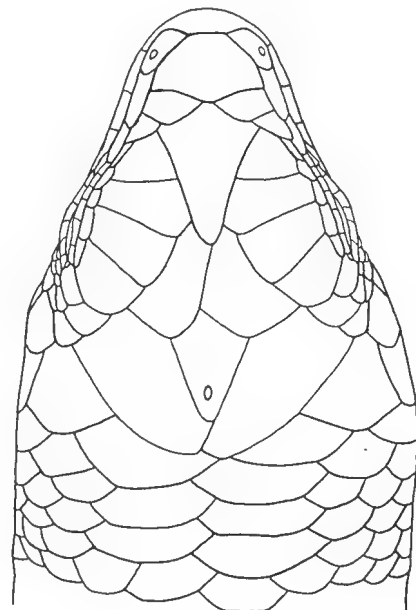


Fig. 5. Dorsal and lateral views of the head of *Calyptotis lepidorostrum* (AM R 59243) from the Blackall Range at Maleny, Qld.

parietals in broad contact behind interparietal; each parietal bordered posterolaterally by large upper secondary temporal, anteriormost nuchal (which is always transversely enlarged) and usually a slightly smaller scale intercalated between the two.

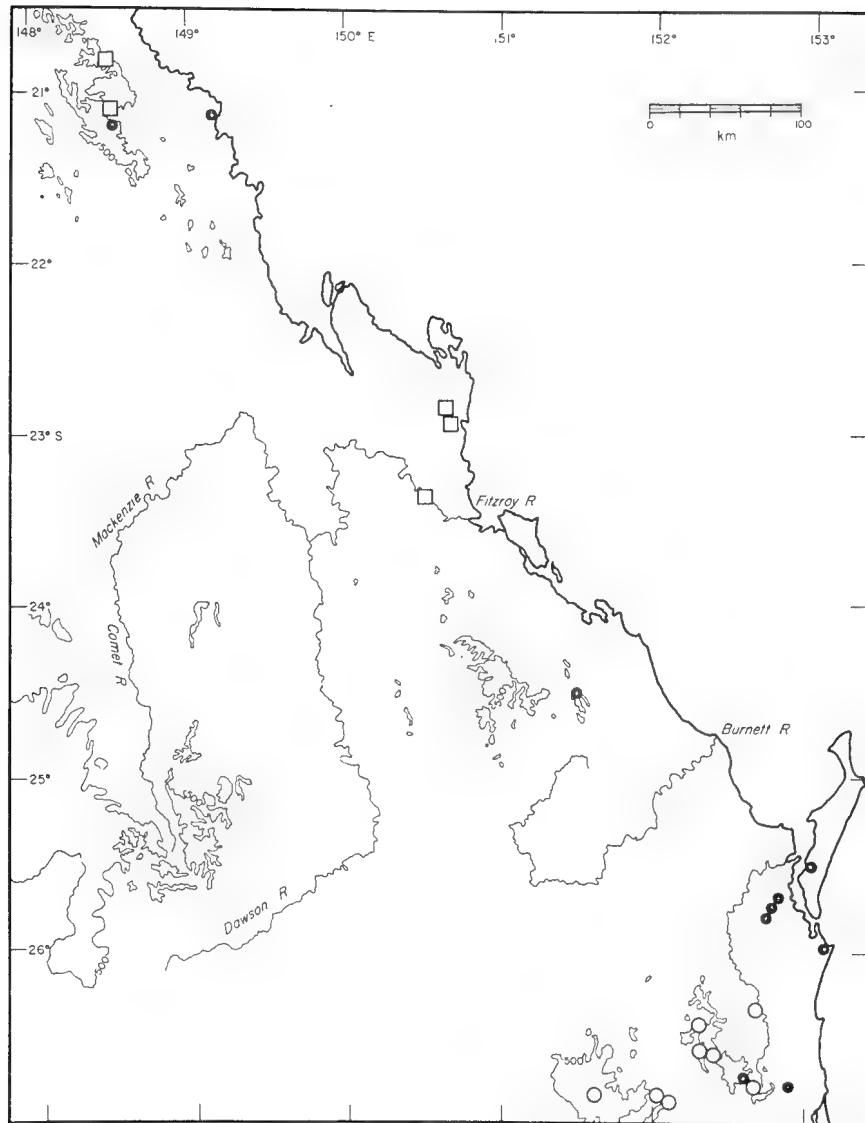


Fig. 6. Map of central eastern and south-eastern Queensland showing the distribution of *Calyptotis lepidorostrum* (black dots) and *C. temporalis* (open squares) and the extreme northern part of the distribution of *C. scutirostrum* (open circles). The contour line is 500 m.

Nasal moderate, widely separated from its fellow, with nostril centrally situated; loreal single, equal to or larger than nasal; preoculars two; supraciliaries six to eight (mode = seven), first and last largest; postoculars two; suboculars series complete, comprising five scales, third of which is small and partially incorporated into eyelid; lower eyelid scaly; supralabials six, fourth below centre of eye; primary temporal single; secondary temporals two, dorsal much larger than ventral, which is about equal in size to primary temporal; external ear opening absent, represented by scaly conical depression; infralabials four, only first in contact with postmental; mental followed by postmental and single pair of chin scales in medial contact (Fig. 5).

Transversely enlarged nuchals 1–5, (\bar{X} = 2.6, mode = 3) on each side, body scales smooth, in 20–24 (\bar{X} = 20.6, mode = 20) longitudinal rows at

midbody; scales in paravertebral rows slightly to appreciably wider than those in more lateral rows, 50–63 (\bar{X} = 55.7) in a single row; medial pair of preanals greatly enlarged; each preanal overlaps preanal lateral to it and is in turn overlapped by preanal medial to it; medial row of subcaudals slightly wider than more lateral row.

Digits moderate in length; fourth toe only slightly longer than third and covered by two longitudinal scale rows for most of length (two most distal scales are single); subdigital lamellae on fourth toe with keels that begin as rounded tubercles basally, become obtuse ridges over the middle length and are lost distally, 8–14 (\bar{X} = 11.0, mode = 11).

Snout–vent length 23–55 mm; tail length 30–69 mm; tail length 1.17–1.50 times SVL; front leg .14–.23 and rear leg .21–.29 times SVL.

Presacral vertebrae 29; phalangeal formulae for manus and pes 2-3-4-4-3 and 2-3-4-5-3 respectively.

Colour in preservative. Dorsum light to dark brown with darker brown spots and blotches scattered more or less randomly on the head and tail but generally aggregated into stripes through the centres of the four dorsalmost scale rows on the body. These stripes are especially distinct and continuous anteriorly but become more diffuse and discontinuous posteriorly. A dark dorsolateral stripe begins in front of the eye and extends posteriorly onto the tail. The stripe is most distinct on the nape and shoulder and becomes diffuse posteriorly. Flanks pale brown to light grey, often with darker brown spots and blotches scattered evenly throughout and a few white spots scattered along the neck and shoulder. Sides of head and labial areas generally with dense dark spots and streaks, although the centres of the labials are generally clear.

There is coarse brown spotting on the sides of the chin and throat in a few of the larger specimens, but there appears to be no sexual difference in its distribution ($X^2 = 0.26$ NS, $N = 74$). There is often fine brown spotting on the underside of the tail and this is more frequent in females than in males ($X^2 = 13.14^{***}$, $N = 70$).

Colour in life. Large individuals of this species usually have bright ventral colours comprising a yellow on the underside of the body and in some individuals a bright coral pink or red on the underside of the tail and thighs and over the vent.

There are very few notes on the individual occurrence of yellow ventral colour in this species. I made notes on 17 animals collected at Cooloola State Forest on 2-3 May 1976. These show that the three smallest specimens (SVL = 23-27 mm) plus a large female (SVL = 43 mm) apparently had no yellow colour in the venter; four of the five remaining females (SVL = 30-45 mm) had pale yellow colour while the fifth female (SVL = 44 mm) and all the remaining specimens, all of which were males (SVL = 40-47 mm), had slightly stronger yellow colour. These results suggest that juveniles lack yellow ventral colour but that larger individuals generally have some yellow colour and in these the intensity is generally greater in males than in females.

Fairly detailed colour notes are available on the occurrence of the coral red tail colour in an expanded sample ($N = 37$) collected at Cooloola State Forest on 2-3 May 1976. These show that no individual smaller than 37 mm SVL ($N = 9$) had appreciable pink colour in the tail but that 11 males larger than 37 mm SVL (40-47 mm) had intense coral pink colour while only five of the 14 females larger than 37 mm (38-48 mm) had similarly intense pink colour. The difference in the frequency of intense colour between the sexes in the larger animals is significant ($P < .001$, Fisher Exact Probability Test). The pink colour apparently also persists better in preservative in males than in females, for after 10 months in preservative all nine males

Table 2. Snout-vent length in mm of the largest individual of each sex of *Calyptotis lepidorostrum* at three different localities. Numbers in parentheses are sample sizes.

	Males	Females
Crediton (920 m)	50 (12)	51 (8)
Bulburin (540-580 m)	52 (8)	54 (6)
Cooloola (near sea level)	47 (14)	48 (17)

retained this colour in the tail but none of the females did.

Details of holotype. The holotype (QM J 33612) is a male with a snout-vent length of 52 mm and a tail length of 61 mm, of which 15 mm is regenerated; prefrontals present and separated; supraciliaries 7/7; enlarged nuchals 3/3; midbody scale rows 20; paravertebrals 54 and subdigital lamellae 11/11.

Etymology. The name *lepidorostrum* derives from the Greek word for scale (*lepidos*) and the Latin word for snout (*rostrum*) and calls attention to the presence of distinct prefrontal scales in contrast to their absence in the closely related *C. scutirostrum*.

Size. There is some indication that females attain a slightly larger size than males in *C. lepidorostrum*. The evidence for this comes from the three largest samples available: Crediton, Bulburin and Cooloola. In all three the largest females are 1-2 mm longer than the largest males (Table 2).

It is interesting to note that individuals from the two montane populations at Crediton and Bulburin appear to attain a slightly larger size than individuals from the lowland population at Cooloola (Table 2). They also appear to be somewhat darker in colour.

Variation in prefrontal scales. Variation in the presence of prefrontals (the sole diagnostic trait separating this species from *C. scutirostrum*) is minimal. Distinct prefrontals are present in all specimens except two from Bulburin State Forest near the centre of the species' distribution: QM J 33752 has the left prefrontal completely fused to the frontonasal and AM R 76194 has the right prefrontal partially fused.

The prefrontals are almost invariably separated from each other (.95, $N = 88$) and in the few cases (.05) in which they do meet, the contact is usually very narrow.

Distribution. *Calyptotis lepidorostrum* ranges along the coast and eastern highlands of central and south-eastern Queensland from the vicinity of Mackay and Eungella National Park south to the Conondale and Blackall Ranges (Figs 6, 14). In the south the range overlaps slightly or interdigitates with the range of *C. scutirostrum*. In the north the range appears to overlap broadly the range of *C. temporalis*, but there are very few localities known as yet for either species in this area and the local distribution patterns remain to be determined.

Habitat. This species appears to be largely, but not exclusively, an inhabitant of rainforest. The species has been collected in fairly large numbers at three sites

representing different localities and elevations in the species' total distribution.

In the northern part of its distribution, *C. lepidorostrum* was encountered at the Crediton site in the Australian Museum and Queensland Museum's joint faunal survey of eastern Australian rainforest. This site—number 7 in the survey—lies at an altitude of 920 m and is covered in wet complex notophyll vine forest on basalt. *C. lepidorostrum* (identified as "*scutirostrum*" in the survey reports) was scored as "abundant" while the only other skink encountered, an undescribed *Lampropholis* in the *delicata* group, was scored as "very abundant" (Anonymous, 1976 and Broadbent and Clark, 1976).

The species was also found near the centre of its range at the two geographically close survey sites in Bulburin State Forest. These sites—numbers 1 and 3—in the survey lie at 540 and 580 m and are covered by wet complex notophyll vine forest and moist low microphyll vine forest respectively. *C. lepidorostrum* (again identified as "*scutirostrum*") was scored as "very abundant" at the first site and "common" at the second. Seven other species of skink were also taken in association with *C. lepidorostrum* at the combined localities: *Anomalopus ophioscincus*, *A. verreauxi*, *Egernia frerei*, a *Lampropholis* of the *delicata* group, *Sphenomorphus quoyi*, *S. tenuis* and *Tiliqua gerrardi* (Anonymous, 1976 and Broadbent and Clark, 1976).

Near the southern end of the its range the species has been encountered in large numbers at Cooloola State Forest in the near sea level vine forests on the white sands for which the area is famous. A single *Anomalopus ophioscincus* and several individuals of a *delicata* species group *Lampropholis* were also encountered in association with *Calyptotis lepidorostrum* (pers. obs.)

The southern end of the species' range appears to be in the area of the Blackall and Conondale Ranges south of Gympie. Here the distribution appears to either overlap or interdigitate with that of *C. scutirostrum*. In a published account of this area, Czechura (1976) suggested that the two species occurred sympatrically in the rainforests of the Conondale Range. Further

work, however, has shown that habitat separation is virtually complete at the local level with *C. lepidorostrum* inhabiting rainforest and *C. scutirostrum* open (sclerophyll) forest. *C. scutirostrum* may, however, occur "in and around margins of rainforest where it abuts open forest formations", and both species may also occur together in the Blackall Ranges in the small remnant pockets of rainforest. It is interesting to note, however, that in the Gallangowan State Forest which is just north of the Conondale and Blackall Ranges and also just north of the northern limit of the range of *C. scutirostrum*, *C. lepidorostrum* occurs in wet sclerophyll forest (Czechura, pers. comm.).

The apparent nearly complete habitat separation in the small area of moderately undisturbed habitats where *C. lepidorostrum* and *C. scutirostrum* both occur plus the lack of any evidence of morphological intergradation in the same area are the reasons for treating these two very similar forms as species.

Reproduction. There are ten gravid females among the available specimens. Eight of these contain only enlarged ovarian eggs. One of these eight lacks a specific date of collection but the others were collected on 23(1) and 27(6) September 1978. The remaining two females contained shelled oviducal eggs, which indicates that the species is oviparous. These two females were collected on 13 October and 14 December (Table 3). The mean SVL of the ten females was 48.5 mm and their mean brood size 3.2. The correlation between SVL and brood size is not significant ($r = .48$, NS, $N = 10$).

There is a large series of specimens from Crediton collected in the period 15–22 April 1975 and another from Cooloola collected on 2–3 May 1976. Both series contain a number of females, seven and 12, respectively, as large as or larger than the smallest known gravid female for the species (39 mm), but none is gravid. These data suggest that the females in these populations were reproductively quiescent at the time of collection.

Sex ratio. The two most thoroughly collected populations are those at Bulburin and Crediton. The numbers of males and females at these two localities were 22 and 17 and 15 and 18, respectively. In neither case does the sex ratio differ significantly from 1:1.

Table 3. Summary of information on the gravid specimens of *Calyptotis lepidorostrum*. The superscript "o" indicates enlarged ovarian eggs (in contrast to oviducal eggs) and the letters "R" and "L" indicate right and left ovaries and oviducts respectively. All localities are in Queensland.

Specimen	Locality	Date	SVL (mm)	Brood Size
AM R 76222	Jimna Forest, Conondale Ra.	23 Sept 1978	50	1R-1L = 2 ^o
AM R 76296	Bulburin State Forest	27 Sept 1978	47	1R-2L = 3 ^o
AM R 76297	Bulburin State Forest	27 Sept 1978	48	2R-2L = 4 ^o
AM R 76299	Bulburin State Forest	27 Sept 1978	50	2R-2L = 4 ^o
AM R 76200	Bulburin State Forest	27 Sept 1978	54	2R-2L = 4 ^o
AM R 76201	Bulburin State Forest	27 Sept 1978	55	2R-2L = 4 ^o
AM R 76202	Bulburin State Forest	27 Sept 1978	51	2R-2L = 4 ^o
QM J 31575	Fraser I. Nat. Park	13 Oct 1978	40	2R-1L = 3
QM J 35878	Tuan State Forest	14 Dec 1977	51	1R-1L = 2
QM J 22274	Coomboo Lake, Fraser I.	1972	39	1R-1L = 2 ^o

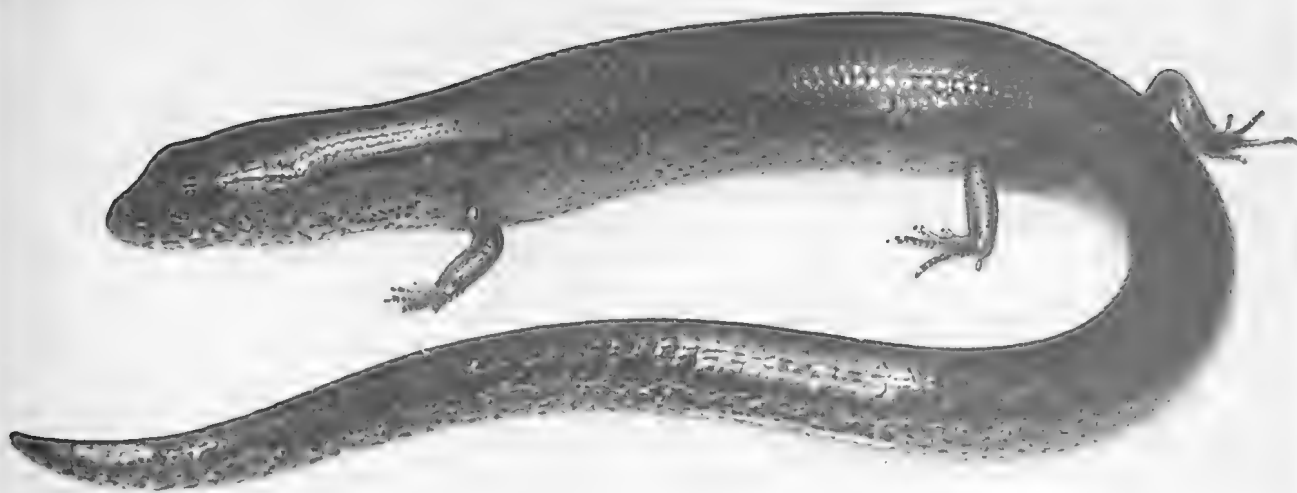


Fig. 7. *Calyptotis scutirostrum* from the Conondale Ranges, south-eastern Queensland.

Comparison with other *Calyptotis*. Comparison between *C. lepidorostrum* and *C. ruficauda* has been made on p. 34.

Calyptotis lepidorostrum is very similar to *C. scutirostrum* except that it possesses prefrontals instead of lacking them.

Calyptotis lepidorostrum differs from *C. temporalis* in having the posteriorly projecting process from the posteromedial corner of the palatal ramus of the pterygoid short instead of long; prefrontal scales present instead of absent; external ear indicated by a scaly conical depression instead of a naked tympanum; secondary temporals two instead of one; fourth toe slightly longer than third instead of subequal; phalanges in the fourth toe of the pes five instead of four; more subdigital lamellae on the fourth toe (8–14, $\bar{X} = 11.0$, $N = 88$ vs 8–10, $\bar{X} = 9.0$, $N = 8$; $t = 4.15^{***}$); more paravertebrals (50–63, $\bar{X} = 55.7$, $N = 46$ vs 46–50, $\bar{X} = 47.8$, $N = 8$) and more presacral vertebrae (29 vs 26).

Calyptotis lepidorostrum differs from *C. thorntonensis* in having the external ear opening indicated by a scaly, conical depression instead of a scaly, discoidal depression (scaly, superficial tympanum); postorbital bone present instead of absent; fewer midbody scale rows (20–24, $\bar{X} = 20.6$, $N = 87$ vs 24, $N = 5$); fourth toe slightly longer than third instead of subequal, and phalanges of fourth and fifth toes of pes five and three, respectively, instead of four and four.

Additional comparisons are provided in Table 5.

Calyptotis scutirostrum (W. Peters, 1873)

Figs 7, 8

Lygosoma scutirostrum W. Peters, 1873: 743. Type locality: Port Bowen.

Cophoscincus obscurus O'Shaughnessy, 1874: 35. Type locality: Queensland.

Calyptotis flaviventer De Vis, 1886: 57–58. Type localities: Breakfast Creek and Macleay Island, Moreton Bay.

Diagnosis. *Calyptotis scutirostrum* differs from all other species of *Calyptotis* in combining the absence of prefrontal scales with the presence of a scaly, conical auricular depression.

Description. Although the original descriptions of *Calyptotis scutirostrum* and its synonyms are fairly good by modern standards, a redescription of the species and a figure of the head (Fig. 8) will facilitate comparisons with the other species described in this paper.

Calyptotis scutirostrum is a medium-sized (maximum SVL–59 mm), light to dark brown skink with non-overlapping, pentadactyl limbs and a dorsal colour pattern comprising a rough-edged, dark dorsolateral stripe on the neck and shoulder and a line of dark spots and dashes along the centre of each of the four dorsalmost longitudinal scale rows (Fig. 7).

Snout moderately short and deep; rostral projecting slightly between nasals; frontonasal usually large (due to incorporation of prefrontals), wider than long; prefrontals usually absent, but small and almost invariably separated when present (see below); frontal slightly shorter than midline length of frontoparietals and interparietal; supraoculars four, anterior two in contact with frontal; frontoparietals distinct, each equal to or slightly larger than interparietal in total area; interparietal distinct, with small clear parietal eye spot posteriorly; parietals in broad contact behind interparietal; each parietal bordered posterolaterally by upper secondary temporal, anteriormost nuchal (which is always transversely enlarged) and usually a slightly smaller scale intercalated between the two.

Nasal moderate in size, widely separated from its fellow, with nostril centrally located; loreal single, equal to or slightly larger than nasal; preoculars two; supraciliaries six to eight (mode = seven) first and last

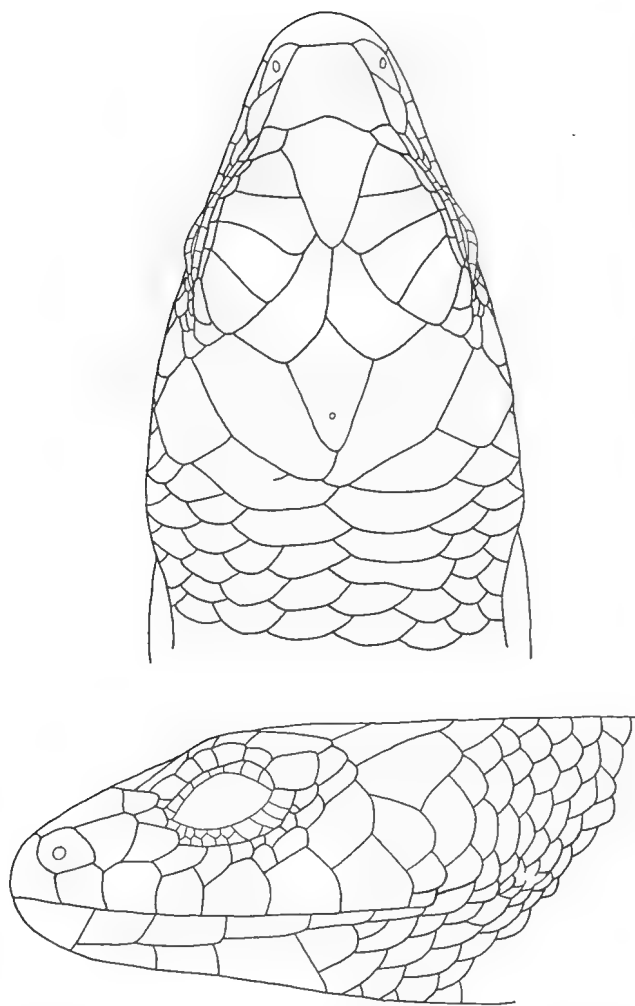


Fig. 8. Dorsal and lateral views of the head of *Calyptotis scutirostrum* (AM R 92088) from 10.4–12.0 km NW of Bostobrick, NSW. In this specimen the postmental and first chin scale are fused on the left side.

largest; postoculars two; subocular series complete, comprising five suboculars, third of which is small and partially incorporated into eyelid; lower eyelid scaly; supralabials six, fourth situated below centre of eye; primary temporal single; secondary temporals two, dorsal much larger than ventral, which is equal in size to primary temporal; external ear opening absent, represented by a scaly, conical depression; infralabials four, first only in contact with postmental; mental followed by postmental and a pair of chin scales in medial contact (Fig. 8).

Transversely enlarged nuchal scales 1–5 (\bar{X} = 2.5, mode = 2) on each side; body scales smooth, in 19–24 (\bar{X} = 20.7, mode = 20) longitudinal rows at midbody; scales in paravertebral rows moderately to appreciably wider than those in more lateral rows, 51–64 (\bar{X} = 55.1) in a single row; medial pair of preanals greatly enlarged; medial row of subcaudals slightly wider than more lateral rows.

Digits short; fourth toe only slightly longer than third, covered above by two longitudinal rows of scales for

most of length (except for two distalmost scales which are single); subdigital lamellae on fourth toe obtusely keeled, 7–13 (\bar{X} = 9.9, mode = 9).

Snout-vent length 26–59 mm; tail length 1.07–1.58 times SVL; front leg .13–.20 and rear leg .18–.29 times SVL.

Presacral vertebrae 29–30; phalangeal formulae for manus and pes 2–3–4–4–3 and 2–3–4–5–3 respectively.

Colour in preservative. The dorsal colour of *C. scutirostrum* in preservative is very similar to that of *C. lepidorostrum* (p.37).

Chin, throat and lateral area of chest with scattered dark spotting (generally more so in females than males; X^2 = 4.57*, N = 137), rest of ventral part of body immaculate; underside of tail with scattered dark spotting in females but largely unspotted in males (X^2 = 30.78***, N = 137).

Colour in life. Larger individuals of *C. scutirostrum* can be fairly colourful on their ventral surfaces: many have some yellow on the ventral part of the body from about the level of the forelegs back and some show a distinct coral red colour on the underside of the tail and thighs and across the vent. The significance of the variation in both the yellow and coral red colour is discussed below.

The most detailed information on the individual occurrence of yellow ventral colour comes from a series of 14 specimens collected by S.J. Copland at Horton's Creek, N.S.W. from 3–5 January 1948. These specimens range from 33 to 43 mm SVL and comprise eight males and six females. All were noted as having yellow colour on the ventral part of the body, but significantly the six largest males (SVL = 38–43 mm) were described as having yellow venters whereas all the females (SVL = 33–43 mm) and the two smallest males (SVL = 36 mm) were described as having pale yellow venters or white venters with a yellowish wash. These observations indicate that, at this time of year at least, yellow colour occurs on the venter of most (all ?) larger individuals and that it is generally most intense in large males.

This conclusion also seems to be supported by less precise observations which I made on a sample collected on 7 February 1976 5.4 km E of Woodenbong, N.S.W. A subset of this sample that I described in the field as having only the "faintest tinge of yellow" on the ventral part of the body comprised two males 30 and 32 mm SVL and 11 females 32–45 mm SVL, whereas the subset I described as "often (with) definite yellow in the venter anterior to the pelvic area" comprised 16 males 32–43 mm SVL and six females 40–44 mm SVL.

The significance of the polymorphism of the coral red colour on the underside of the tail was investigated in five samples collected without any conscious bias in the following localities in northern New South Wales between 7 February and 14 March 1976: 8.1 km W of Drake (N = 81); 5.4 km E of Woodenbong (N = 38); 7.0 km W of Woodenbong (N = 3); 8.0 km E of Woodenbong (N = 16), and 10.4–12.0 km NW of Bostobrick (N = 6). Tail colour in life, snout-vent-

length and sex (based on an examination of gonads) were scored for as many of these specimens as possible ($N = 133$). From these data it was clear that (1) no individual 32 mm SVL or smaller had any red colour in the tail and (2) in individuals 33 mm SVL and larger, males almost invariably had tail colour whereas females almost invariably, but not always, lacked it almost invariably, but not always, lacked it ($X^2 = 82.9^{***}$). The two males scored as lacking tail colour were relatively large (42 and 44 mm SVL) and hence cannot have their lack of tail colour ascribed to young age. Four of the seven females scored as having tail colour in life lost this colour after a period of preservation while all other individuals retain tail colour after being treated similarly, thereby indicating that, when present in females, tail colour is perhaps less strongly developed than in males.

Etymology. Although Wilhelm Peters did not specifically state that the name *scutirostrum* derived from the large frontonasal scale of the type, he described the scale and perhaps sought to emphasize it with this name.

Distribution. *Calyptotis scutirostrum* ranges along the coastal plain and highlands from an area just south of Gympie in south-eastern Queensland to an area just northwest of Dorrigo, New South Wales (Figs 9, 14). The most inland extent of the range is in the Bunya Mountains and the highlands SSW of Stanthorpe.

The range of *C. scutirostrum* overlaps the range of its very similar northern relative *C. lepidorostrum* in the highlands separating the Mary and Burnett drainages to the north and the Brisbane drainage to the south (the highlands encircled by the Bruce, Wide Bay, Burnett and D'Aguilar Highways). To the south, *C. scutirostrum* is separated from *C. ruficauda* by the Dorrigo Plateau.

Variation in prefrontal scales. Due to the fact that the general absence of prefrontal scales is the main character by which *C. scutirostrum* can be distinguished from its northern relative *C. lepidorostrum*, it may be useful to discuss briefly the variation in the occurrence of prefrontals in *C. scutirostrum*.

The overall frequency of prefrontals in *scutirostrum* is low; out of 365 specimens surveyed only 16 (.04) possessed prefrontals and of these only 9 (.02) possessed prefrontals on both sides. Prefrontals are known to occur in populations from the following localities: Toowoomba, Mt. Mitchell, Upper Brookfield, northern Stradbroke Island, Mt. Ballow and Fletcher in Queensland and 8.1 km W of Drake, 10.4–12.0 km NW of Bostobrick and 11.5 km SW of Nymboida in New South Wales. These localities are widely scattered throughout the range of *C. scutirostrum* and show no significant pattern.

Prefrontals occur in different frequencies in different populations. Of 81 specimens collected 8.1 km W of Drake, N.S.W., for example, 10 possess distinct prefrontals whereas none of 37 specimens collected 5.4 km E of Woodenbong, N.S.W. have distinct prefrontals ($P = .02$, Fisher Exact Probability Test).

When prefrontals do occur in *C. scutirostrum* they are generally smaller than in *C. lepidorostrum*. This is

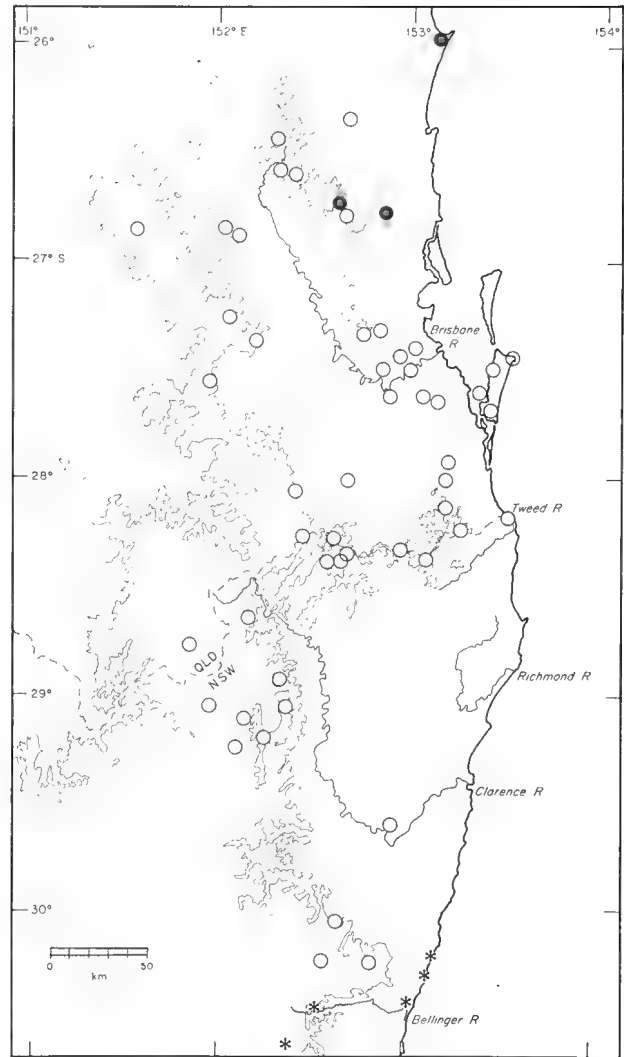


Fig. 9. Map of north-eastern New South Wales and south-eastern Queensland showing the distribution of *Calyptotis scutirostrum* (open circles), the northern part of the distribution of *C. ruficauda* (asterisks) and the southern part of the distribution of *C. lepidorostrum* (black dots). The contour line is 500 m.

especially noticeable when the prefrontals are paired, for then they are generally more widely separated than in *C. lepidorostrum*.

Variation in size. There is evidence that females attain slightly larger size than males in most populations. This is especially evident in the three largest samples mentioned above in conjunction with the analysis of tail colour.

(1) Of the 81 specimens collected 8.1 km W of Drake, N.S.W., 74 could be both accurately sexed and measured. Only two of the 36 males attained a maximum snout-vent length of 45 mm, whereas four of 38 females attained 45 mm snout-vent length and one reached 48 mm.

(2) Of the 38 specimens collected 5.4 km E of Woodenbong, N.S.W., 35 could be both sexed and measured. One of the 18 males attained a maximum snout-vent length of 44 mm, while one of the 17

Table 4. Summary of information on the gravid specimens of *Calypotis scutirostrum*. The superscript "o" indicates enlarged ovarian eggs (in contrast to oviducal eggs) and the letters "R" and "L" indicate right and left ovaries and oviducts, respectively.

Specimen	Locality	Date	SVL (mm)	Clutch Size
QM J 30414	6 km S of Yarraman, Qld		45	1R-1L = 2°
QM J 26720	Mt. Ballow, Qld.	Sept 1975	53	1R-2L = 3°
AM R 76104	5.4 km W of Woodenbong, NSW	19 Sept 1978	41	2R-1L = 3°
AM R 76154	Kingham Rd, Jimna Ra., Qld	24 Sept 1978	43	2R-1L = 3°
AM R 17704	Bunya Mountains, Qld	4-5 Dec 1960	59	4°
AM R 76155	Kingham Rd, Jimna Ra., Qld	24 Sept 1978	50	2R-3L = 5
AM R 43049	11 mi SE Tenterfield, NSW	17 Oct 1972	44	2R-2L = 4
AM R 43050	Crooked Creek, NSW	17 Oct 1972	41	2R-1L = 3
AM R 43055	Rocky River, NSW	17 Oct 1972	42	2R-1L = 3
AM R 43058	1 mi W of Drake, NSW	17 Oct 1972	48	2R-2L = 4
AM R 17702	Bunya Mountains, Qld	4-5 Dec 1960	54	3R-1L = 4
AM R 17705	Bunya Mountains, Qld	4-5 Dec 1960	56	3R-2L = 5
AM R 17706	Bunya Mountains, Qld	4-5 Dec 1960	52	3R-2L = 5
AM R 57533	Wilson's Peak, Qld	10 Dec 1940	52	2R-2L = 4
AM R 57540	Wilson's Peak, Qld	10 Dec 1940	51	2R-2L = 4
AM R 57553	Wilson's Peak, Qld	10 Dec 1940	54	2R-1L = 3
QM J 27365	Stradbroke I., Qld	Jan 1976	37	1R-1L = 2
AM R 57573	Hortons Creek, NSW	3 Jan 1948	42	1R-1L = 2
AM R 57574	Hortons Creek, NSW	3 Jan 1948	43	1R-1L = 2
QM J 2447	Gowrie Scrub, Qld	?	39	Oviducal eggs
QM J 14142	?	?	46	2R-2L = 4
QM J 30415	6 km S of Yarraman, Qld		44	1L = 1

females attained 44 mm SVL and another reached 45 mm.

(3) All 16 specimens collected 8.0 km E of Woodenbong could be sexed and measured. Two of the nine males reached a maximum SVL of 42 mm while two of seven females reached 42 mm SVL and two others reached 43 mm.

In addition to the sexual dimorphism in size, there is also some geographic variation that is interesting. The animals in the Bunya Mountains, for example, seem to reach a larger size than animals from elsewhere. This is evidenced by the fact that out of 261 specimens from throughout the range of *C. scutirostrum* exclusive of the Bunya Mountains, only one (AM R 57553 from Wilson's Peak, SE Queensland) attained a SVL of 54 mm, whereas seven of the 17 specimens from the Bunya Mountains measured 54–59 mm SVL.

Habitat. The available data indicate that *C. scutirostrum* is an inhabitant of both rainforest and moist sclerophyll forest, although personal experience indicates that it is much more common in the latter than in the former.

The habitat associations of *C. scutirostrum* and its close relative *C. lepidorostrum* in their narrow zone of overlap in south-eastern Queensland are discussed in the "Habitat" section of the *C. lepidorostrum* account.

Reproduction. In an effort to learn something about the mode of reproduction, brood size and time of reproduction, the available specimens were examined for gravid females. A total of 22 gravid females was found: five with enlarged, yolky ovarian eggs and 17 with shelled oviducal eggs (Table 4). The texture of the

shell in the latter indicated that the species is almost certainly oviparous.

The 21 females in which clutch size could be determined ranged in size from 37–59 mm SVL ($\bar{X} = 47.5$) and as the smallest individual had oviducal eggs, her size may be taken as approximately the size at the onset of maturity. The number of eggs in these females ranged from 2 to 5 ($\bar{X} = 3.6$) and there was a positive correlation between female size and clutch size ($r = 0.66^{**}$). The earliest collection date for a gravid female was for one specimen carrying ovarian eggs: 19 September. The latest dates were for three females carrying oviducal eggs: two collected on 3 January and one collected in "January". In that a very large number of specimens ($N = 123$) were collected from two nearby areas in northern New South Wales on 7–8 February 1976 and not a single gravid female was included, it would appear that, at least in this area, egg laying had ceased by the first week in February.

Sex ratio. The two largest samples mentioned above in the analyses of tail colour and body size also allow an assessment of sex ratio. The larger of the two samples (collected 8.1 km W of Drake) comprised 81 specimens. It was possible to make unequivocal sex determinations on 76 of these specimens, of which 36 were males and 40 females. The smaller sample (collected 5.4 km E of Woodenbong) comprised 37 specimens. Sex was determined for 35 of these and 18 proved to be males and 17 females. It would appear, therefore, that in neither of these populations is there a significant deviation from a 1:1 sex ratio.

Origin of the type specimen of *Calypotis scutirostrum*. The type of *C. scutirostrum* was said to

Table 5. Comparison of certain meristic, mensural and proportional characters in *Saiphos equalis* and the five species of *Calyptotis*.

Character	<i>S. equalis</i>	<i>C. ruficauda</i>	<i>C. lepidorostrum</i>	<i>C. scutirostrum</i>	<i>C. temporalis</i>	<i>C. thorntonensis</i>
Midbody scale rows						
Range	18-22	20-24	20-24	19-24	20-22	24
Mean	19.2	22.1	20.6	20.7	20.6	24
Mode	20	22	20	20	20	24
S.D.	1.01	.65	.98	1.10	.92	—
N	183	59	87	107	8	5
Subdigital lamellae (4th toe)						
Range	2-5	10-15	8-14	7-13	8-10	8-10
Mean	3.3	12.8	11.0	10.0	9.0	8.8
Mode	4	13	11	9	9	9
S.D.	.82	.91	1.34	1.16	.76	.84
N	19	61	88	103	8	5
Paravertebral scales						
Range	64-74	51-59	50-63	51-64	46-50	51-54
Mean	68.9	53.9	55.7	55.1	47.8	53.2
S.D.	2.96	1.86	3.15	2.69	1.75	1.30
N	19	28	46	37	8	5
Supraciliaries						
Range	5-7	6-8	6-8	6-8	7	7-8
Mean	6.8	7.0	7.0	7.0	7.0	7.6
Mode	7	7	7	7	7	8
S.D.	.38	.26	.40	.26	—	.55
N	204	59	87	92	8	5
Nuchals						
Range	1-5	1-4	1-5	2-4	0-4	0-3
Mean	3.8	2.5	2.6	2.6	2.5	1.8
Mode	4	2	3	2	2,3	3
S.D.	.66	.59	.67	.61	.53	1.30
N	91	61	88	97	8	5
Snout-vent length (mm)						
Range	30-85	21-55	23-55	26-59	32-44	29-35
N	307	80	86	220	8	5
Tail length (mm)						
Range	26-103	32-73	30-69	32-74	45-50	32
N	76	32	27	57	2	1
Tail length/snout-vent length						
Range	.97-1.33	1.13-1.53	1.17-1.50	1.07-1.58	1.47-1.59	1.07
N	56	31	26	54	2	1
Length of foreleg (mm)						
Range	3.5-6.0	5.0-10.0	5.0-8.5	6.5-9.5	5.5-7.0	5.5
N	33	33	47	26	7	5
Length of foreleg/snout-vent length						
Range	.06-.11	.17-.25	.14-.23	.13-.20	.16-.19	.16-.19
N	33	33	47	26	7	5
Length of rear leg (mm)						
Range	4.5-9.0	7.0-15.0	6.5-12.5	7.0-13.0	7.5-9.5	7.5-8.0
N	32	32	47	26	7	5
Length of rear leg/snout-vent length						
Range	0.09-0.14	0.24-0.33	0.21-0.29	0.18-0.29	0.21-0.27	0.23-0.27
N	32	32	47	26	7	5

have come from Port Bowen, Queensland, a locality situated at 22°29' S and 150°45'30" E in the present Port Curtis area (Wells, 1848). This area is about 100 km NNE of Rockhampton in what is now a restricted military reserve.

Unfortunately it is difficult to accept this locality as accurate because it lies some 480 km NNW of the range

of *C. scutirostrum* as determined from all other known specimens in Australian museums. One of three explanations may serve to resolve this difficulty.

(1) *C. scutirostrum* does occur north of Amanoor to Port Clinton but has not been collected in the intervening area. This seems unlikely due to the fact that a good deal of collecting has been carried out in the area and

only *C. lepidorostrum* has been found.

(2) The type specimen of *C. scutirostrum* is a *C. lepidorostrum* that lacks prefrontals. This seems unlikely in that the loss of even a single prefrontal is a very rare event in the known populations of *C. lepidorostrum* (p.37).

(3) The type locality is in error and the type specimen was collected further south, perhaps in what is now the greater Brisbane area where *C. scutirostrum* is common. This last explanation seems the most plausible.

Comparison with other *Calyptotis*. Comparisons between *C. scutirostrum* and *C. ruficauda* and *C. lepidorostrum* have been made on pp.34 and 39 respectively.

Calyptotis scutirostrum differs from *C. temporalis* in having the posteriorly projecting process from the posteromedial corner of the palatal ramus of the pterygoid short instead of long; external ear indicated by a scaly, conical depression instead of a naked tympanum; secondary temporals two instead of one; fourth toe slightly longer than third instead of subequal; phalanges in the fourth toe of pes five instead of four; more subdigital lamellae on the fourth toe (7-13, $\bar{X} = 10.0$, $N = 103$ vs 8-10, $\bar{X} = 9.0$, $N = 8$; $t = 2.39^*$); more paravertebrals (51-64, $\bar{X} = 55.1$, $N = 37$ vs 46-50, $\bar{X} = 47.8$, $N = 8$) and more presacral vertebrae (29-30 vs 26).

Calyptotis lepidorostrum differs from *C. thorntonensis* in having the external ear indicated by a scaly, conical depression instead of a scaly, discoidal depression (scaly superficial tympanum); postorbital bone present instead of absent; fewer midbody scale rows (19-24, $\bar{X} = 20.7$, $N = 107$ vs 24, $N = 5$); fourth toe slightly longer than third instead of subequal, and phalanges of fourth and fifth toes of pes five and three respectively, instead of four and four.

Additional comparisons are provided in Table 5.

Specimens examined. The specimens examined in this study are listed below. The arrangement is roughly from north to south and from west to east.

QUEENSLAND. BMNH 1946.81697 (holotype of *obscurus*); NMV 2050; Port Bowen: ZMB 7823 (holotype of *scutirostrum*); Anamoor: AM R 59249; near "The Breadknife", headwaters of Booloumba Creek, Conondale Range: AM R 59250-59251; Gallangowan: AM R 59257; Gheerulla Creek: AM R 59252; Bunya Mountains: AM R 17702-17707, 21279, 26148, QM J 12188-12189, 23932, QNP 294, 301, 735; Marlaybrook: QM J 27522; Bunya Mountains National Park: QM J 27531-27533, 27535, 27546; approximately 4-5 km SE of Yarraman township, Yarraman State Forest: QM J 26129-26130, 26134; 6 km S of Yarraman: QM J 30414-30416; Blackbutt: AM R 59247-59248; Crows Nest: AM R 26116; Mt Glorious: AM R 26141, QM J 23703; Ravensbourne National Park: QNP 248, 736-737, 740-742; Ravensbourne: QM J 30615-30630; 24.5 km NNW of Mt. Nebo: AM R 92071; Mt. Sampson, Sampsonvale: QM J 3281-3282; Upper Brookfield: AM R 32720; Mt. Cootha: QM J 22969, 23658; Brisbane: QM J 1305, 12190; Aspley: QM J 20221-20222; Auchenflower: QM J 14390-14391; Enoggera: QM J 12185; Indooroopilly: QM J 15803; Stafford Heights: AM R 60997-60999; St. Lucia: MVZ 74779,

QM J 12177, 12184; The Gap: QM J 21371; Virginia: QM J 21426, 21437-21439; Wavell Heights: QM J 21447-21448, 21666; Zillmere: QM J 21941; Slacks Creek: QM J 12178-12179; Point Lookout, Stradbroke Island: QM J 27365; near Point Lookout: QM J 24170; Brown Lake: QM J 24077; pumping station near Dunwich: QM J 24093; 5 mi N of south end of North Stradbroke: QM J 22018; Goodna Scrub: QM J 3147-3148; near Steep Hill, Daisy Hill State Forest via Rochedale: QM J 29925; Gowrie Scrub: QM J 2446-2451; Toowoomba: AM R 54283-54284, QM J 2644-2646, 3031-3036; Cunningham's Gap: QNP 154-155; Boonah: WAM 48131-48139; 1 mi from Eagle Heights: QM J 12182-12183; Mt. Tamborine: QM J 1102-1104, 13913-13916, 13918, 18021, SAM 3365 A-C; Beechmont: QM J 13936; about 29 mi E of Warwick: AM R 54278; Emu Vale: QM J 14316-14317; Upper Emu Creek at foot of Mt. Superbus: QM J 30523-30533; Wilson's Peak: AM R 57533-57553; Mt. Ballow: QM J 26720-26721; Mt. Gipps: AM R 59254-59256; Lamington National Park: QM J 22056, 26896; McPherson Mts: CAS 77097; Springbrook: QM J 21665, QNP 272; Currumbin Creek: QM J 12186-12187; Fletcher: NMV 103, 5690-5693; Wyberba: QM J 13933.

NEW SOUTH WALES. 8.0 km E of Woodenbong: AM R 92072-92087; 5.4 km E of Woodenbong: AM R 92030-92067; 7.0 km W of Woodenbong: AM R 92068-92070; Richmond River: AM R 869; Undercliffe Falls: AM R 59253, 59258; 1 mi W of Drake: AM R 43057-43059; 8.1 km W of Drake: AM R 90387-90453, 92015-92029; 8 mi S of Drake: AM R 43052; Crooked Creek, 25 mi NE of Tenterfield: AM R 43050-43051; 5 mi W of Tenterfield: AM R 35206-35212; 11 mi SE of Tenterfield: AM R 43049; 16 mi SE of Tenterfield: AM R 43056; Rocky River, 23 mi ESE of Tenterfield: AM R 43054; 7 mi E of Sandy Flat: AM 43060-43061; between Clarence River and Grafton: QM J 26145-26146; Horton's Creek at West's Camp near junction with Cloud's Creek, 5 mi from Nymboida on Tyringham road: AM R 57569-57582; 11.5 mi SSW of Nymboida (by road): AM R 57554-57568; 14 mi NW of Dunburrabin: AM R 43046-43048; 10.4-12.0 km NW of Bostobrick Post Office: AM R 92088-92093.

LOCALITY UNKNOWN. AM 6347, QM J 12180.

Calyptotis temporalis n.sp.

Figs 10, 11

Holotype. Queensland Museum J 32594: 9.15 km W of the Cathu State Forestry Office via the road to the native pine plantation in the Clarke Range and then 1.5 km anticlockwise on the plantation loop road, Cathu State Forest, central-east Queensland; or, more approximately, about 9 km SW of Elaroo, Qld. Altitude 685 m. Collected by A. Greer on 17 August 1976. The coordinates of the type locality are 20°49'S, 148°31'E.

Paratypes. All localities are in Queensland.

Australian Museum R 60763-60764: same data as holotype; R 60765: east side of Pistol Gap, approximately 22.6 km N of Yeppoon (from the junction of the Esplanade road and the road to Rockhampton) via the Byfield road, Queensland. Altitude <76 m. Collected by A. Greer on 22 August 1976. Queensland Museum J 13718: Rockhampton; J 25742-25743: Byfield; J 34089: Finch Hatton National Park; J 35088, 35121: 6 km along Cameron Road, Eungella.



Fig. 10. *Calyptotis temporalis* from the Clark Range, Qld.

Diagnosis. *Calyptotis temporalis* differs from the congeners in each of the following two characters: a single secondary temporal instead of two and a single row of scales covering the fourth toe instead of two or more.

Description. *Calyptotis temporalis* is a small (maximum SVL = 36 mm) dark brown skink with relatively short, nonoverlapping pentadactyl limbs and a dark dorsolateral stripe that extends the length of the neck and body but is most strongly developed on the neck and anterior part of the body (Fig. 10).

Snout moderately short and deep; rostral projecting slightly between nasals; frontonasal large (undoubtedly due to incorporation of prefrontals), wider than long; prefrontals absent; frontal shorter than midline length of frontoparietals and interparietal; supraoculars four, anterior two in contact with frontal; frontoparietals distinct, each slightly larger than interparietal in total area; interparietal distinct, with small clear parietal eye spot posteriorly; parietals in broad contact behind interparietal; each parietal bordered posterolaterally by upper secondary temporal, anteriormost nuchal (which is generally transversely enlarged) and usually one or two smaller scales intercalated between the two.

Nasal moderate, separated from its fellow, with nostril centrally located; loreal single, equal to or slightly larger than nasal; preoculars two; supraciliaries seven, first and last largest; postoculars two; suboculars five, in continuous series below eye; lower eyelid scaly; supralabials six, fourth situated below centre of eye; primary temporal single; secondary temporal single, very large; external ear opening large, circular; tympanum only slightly recessed (more so along its posterior edge), scaleless, moderately to heavily pigmented; infralabials four, first in contact with postmental; mental followed by postmental and a pair of chin scales in medial contact (Fig. 11).

Transversely enlarged nuchals 0-3 (\bar{X} = 2.5, mode = 3) on each side; body scales smooth, in 20-22 (mode = 20) longitudinal rows at midbody; scales in paravertabral rows slightly wider than those in more lateral rows, 46-50 (\bar{X} = 47.8) in a single row; medial

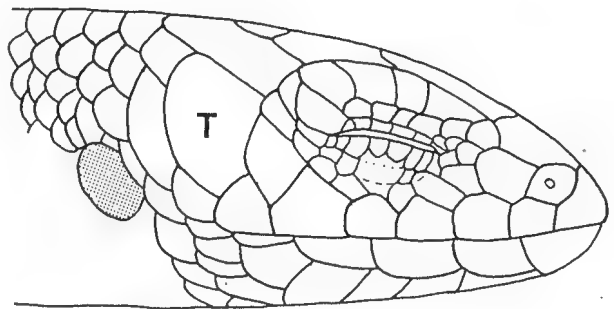
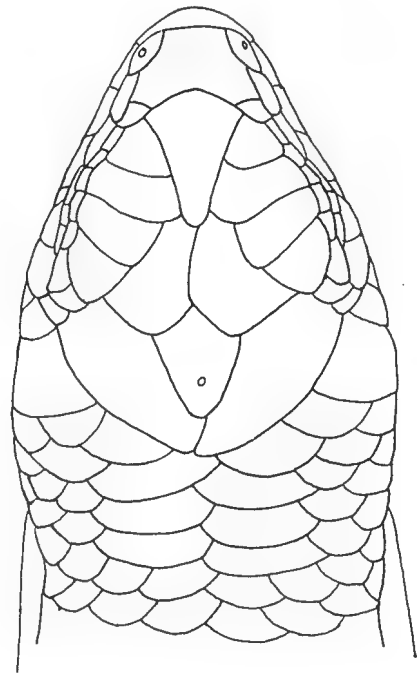


Fig. 11. Dorsal and lateral views of the holotype of *Calyptotis temporalis* (QM J 32594) from Cathu State Forest in the Clark Range, central-eastern Queensland. Note the single large secondary temporal scale (T) which is diagnostic for the species.

pair of preanals greatly enlarged; each preanal overlaps preanal lateral to it and is overlapped by preanal medial to it; medial row of subcaudals slightly wider than more lateral rows.

Digits short; fourth toe equal to or slightly shorter than third and covered above by a single row of scales; subdigital lamellae on fourth toe single with rounded tubercles basally and obtuse keels distally, 8–10 (\bar{X} = 9.0, mode = 9).

Snout–vent length 32–36 mm; tail length 1.47–1.59 times SVL; front leg .16–.19 and rear leg .21–.27 times SVL.

Presacral vertebrae 26; phalangeal formulae for manus and pes 2–3–4–4–3 and 2–3–4–4–3 respectively.

Colour in preservative. Dorsum brown with aggregations of dark brown scattered over the head, generally along the suture lines, and coalesced into broken longitudinal stripes through the centres of the four most dorsal scale rows on the body; a dark brown dorsolateral stripe extends from the posterior corner of the eye to the base of the tail and is confined to the lower part of the third dorsal scale row and the upper part of the fourth at midbody; sides light brown flecked with dark brown; venter immaculate, except for scattered brown spotting on the chin, throat and neck.

Colour in life. Colour notes are available for only four specimens as follows:

AM R 60763 is a 33 mm SVL female which is reproductively inactive, to judge from its small ovaries and oviducts; in life this specimen showed no ventral colour.

AM R 60764 is a 34 mm SVL male with relatively small testes; it showed no ventral colour on the underside of the body in life but did show faint coral pink colour on the underside of the tail.

QM J 32594, the holotype, is a 35 mm SVL male with very large testes; it showed yellow ventral colour from the level of the forelegs posteriorly to the vent and coral pink colour from the level of the vent posteriorly throughout the length of the tail.

AM R 60765 is a 36 mm SVL female with large ovarian eggs; it had yellow on the ventral part of the body and no colour on the underside of the tail.

From these limited data it would appear that mature, and perhaps only reproductively active, individuals have ventral coloration and that this comprises a yellow venter in females and a yellow venter and coral pink underside to the tail in males.

Details of holotype. The holotype (QM J 32594) is a male with a snout–vent length of 35 mm and a tail length of 39 mm, of which 18 mm is regenerated; supraciliaries 7/7; enlarged nuchals 4/4; midbody scale rows 20; paravertebral scales 46, and subdigital lamellae 10/8.

Etymology. The name *temporalis* refers to the single deep secondary temporal that distinguishes this species from all other *Calypotis*.

Distribution. To date the species is known only from Rockhampton, the Byfield area (NE of

Rockhampton), Finch Hatton National Park (W of Mackay), and Cathu State Forest (SSW of Proserpine) in central east Queensland (Figs 6, 14).

Altitudinally the species ranges from the lowlands of the Byfield area up to at least 685 m in the Clarke Range of Cathu State Forest.

Although the general distributions of *C. temporalis* and *C. lepidorostrum* appear to overlap broadly in the area between the Pioneer drainage in the north and the Rockhampton area in the south, the known localities for the two species are very few, and the local distribution patterns remain to be determined. The parapatric distributions of *C. lepidorostrum*, *C. scutirostrum* and *C. ruficauda* in the south raise the question of whether such a distributional relationship may not also hold for *C. temporalis* and *C. lepidorostrum* in the north.

Habitat. The three specimens from the Clarke Range at Cathu State Forest (AM R 60763–60764 and QM J 32594) were in a small patch of high altitude rainforest which was surrounded on three sides by an immense Hoop Pine plantation and cut off from extensive rainforest on the fourth side by the plantation's service road. A small creek drains this small patch of rainforest and then immediately enters the much larger Plantation Creek, which in turn quickly passes under the service road and into the extensive rainforest. All three specimens were among the loose roots beneath flat stones on a rather steep bank just above the small tributary creek. The bank received partial afternoon sunlight and was moderately moist. *Taudactylus eungellensis* were abundant under the small rocks at the edge of the creek and two *Lampropholis basiliscus* were found in the forest near the creek.

The single specimen from the east side of Pistol Gap on the road to Byfield (AM R 60765) was on very dry soil under a log just above a small dry creekbed. The vegetation along the creek comprised an open depauperate rainforest with sclerophyll elements. The creekbed led into a *Melaleuca* swamp while the surrounding upland vegetation was open sclerophyll forest. The entire area was very dry at the time of collection and the only other reptile collected was a *Carlia pectoralis*.

The two Byfield specimens (QM J 25742–25643) were collected under logs in rainforest, and the single specimen from Finch Hatton National Park (QM J 34089) was collected in leaf litter at site number 9 in the Australian Museum and Queensland Museum's joint faunal survey of eastern Australian rainforests. This site lies at 180 m and is covered with wet complex notophyll vine forest. The specimen was tentatively identified as "*Sphenomorphus scutirostrus*" in the survey's preliminary reports (Anonymous, 1976 and Broadbent and Clark, 1976) and was said to have been "very abundant", although only a single specimen appears to have been collected. Other skinks recorded at the same site were an unidentified species of *Anomalopus*, *Carlia rhomboidalis*, a member of the

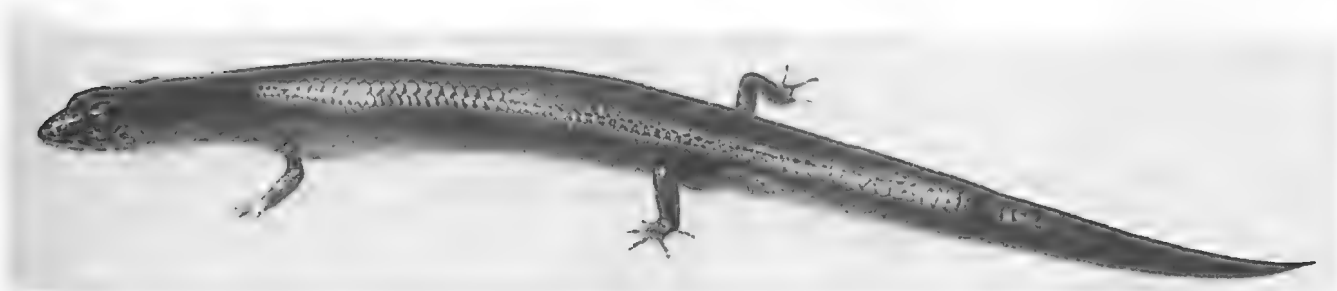


Fig. 12. *Calyptotis thorn-tonensis* from Thornton Peak, north-eastern Queensland.

Lampropholis challengerii complex, a member of the *Lampropholis delicata* complex, *Sphenomorphus amplius*, *S. quoyii* and *S. tenuis*.

Reproduction. The only gravid female in the small series is AM R 60765. This animal has a SVL of 36 mm and contains two large yolky ovarian eggs, one in each ovary. The largest male in the series (QM J 32594) has very large testes. Both animals were collected in the third week in August and both appear to have been in reproductive condition.

Comparison with other *Calyptotis*. Comparisons between *C. temporalis* and *C. ruficauda*, *C. lepidorostrum* and *C. scutirostrum* have been made on pp.34, 39, and 44, respectively.

Calyptotis temporalis differs from *C. thorn-tonensis* in having the posteriorly projecting process from the posteromedial corner of the palatal ramus of the pterygoid moderately long instead of short; the head and body moderately deep instead of depressed; prefrontals absent instead of present; external ear represented by a naked tympanum instead of a scaly, discoidal depression (scaly superficial tympanum); phalanges in the fourth toe of the manus four instead of three, and phalanges in the fifth toe of the pes three instead of four; fewer midbody scale rows (20–22, \bar{X} = 20.6, N = 8 vs 24, N = 5); and fewer paravertebrals (46–50, \bar{X} = 47.8, N = 8 vs 51–54, \bar{X} = 53.2, N = 5).

Additional comparisons are provided in Table 5.

Calyptotis thorn-tonensis n.sp.

Figs 12, 13

Holotype. QM J 28354. Southern base of Thornton Peak, NE Queensland. Altitude 640 mm. Collected by W. Boles, E. Cameron, H.G. Cogger and P. Webber on 27 July 1976. The coordinates of the type locality are 16°11'S, 145°24'E.

Paratypes. AM R 56575–56577, 56603. Same data as holotype.

Diagnosis. *Calyptotis thorn-tonensis* differs from its congeners in each of the following characters: a more depressed head and body; external ear represented by a scaly, discoidal depression (scaly, superficial tympanum) instead of either a scaleless tympanum or a scaly conical depression, and generally more longitudinal scale rows at midbody (24 vs modes of 22 or 20).

Description. *Calyptotis thorn-tonensis* is a small (maximum SVL = 35 mm) slightly depressed, dark brown skink with relatively short, nonoverlapping pentadactyl limbs, a finely mottled light and dark brown dorsum and a diffuse dark dorsolateral stripe, which is most pronounced on the neck and shoulder (Fig. 12).

Snout short and depressed; rostral projects moderately onto dorsal surface of snout due to depression of head but projects only slightly between nasals; frontonasal about as wide as long; prefrontals present, moderately well developed and separated medially; frontal much longer than wide, shorter than midline length of frontoparietals and interparietal; supraoculars four, anterior two in contact with frontal; frontoparietals distinct, each equal to or smaller than interparietal in total area; interparietal distinct, with conspicuous light parietal eye spot posteriorly; parietals in broad contact behind interparietal; each parietal bordered posterolaterally by a relatively long, thin upper secondary temporal, anteriormost nuchal (which is generally transversely enlarged) and generally a smaller scale intercalated between the two.

Nasal moderate in size, separated from its fellow, with nostril centrally situated; loreal single, equal to or slightly larger than nasal; preoculars two (larger and lower of two generally reaches the supralabial series but may be 'cut off' by the anterior extension of the first subocular); supraciliaries seven to eight (mode = eight); postoculars one or two; subocular series complete, comprising six scales; lower eyelid scaly; supralabials six, fourth situated below centre of eye; primary temporal single; secondary temporals two, dorsal long and thin, ventral rhomboidal and larger than primary temporal; tympanum superficial, circular, scaly; infralabials four, first only in contact with postmental; mental followed by postmental and a pair of chin scales in medial contact (Fig. 13).

Transversely enlarged nuchals 0–3 (\bar{X} = 1.6, mode = 1) on each side; body scales smooth, in 24 longitudinal rows at midbody; scales in paravertebral rows only slightly wider than those in more lateral rows, 51–54 (\bar{X} = 53.20) in a single row; medial pair of preanals very large, each preanal overlaps the preanal lateral to it and is overlapped by the preanal medial to it; medial row of subcaudals slightly wider than those in more lateral rows.

Digits short; fourth toe equal to or slightly shorter than third, covered by two rows of scales for most of

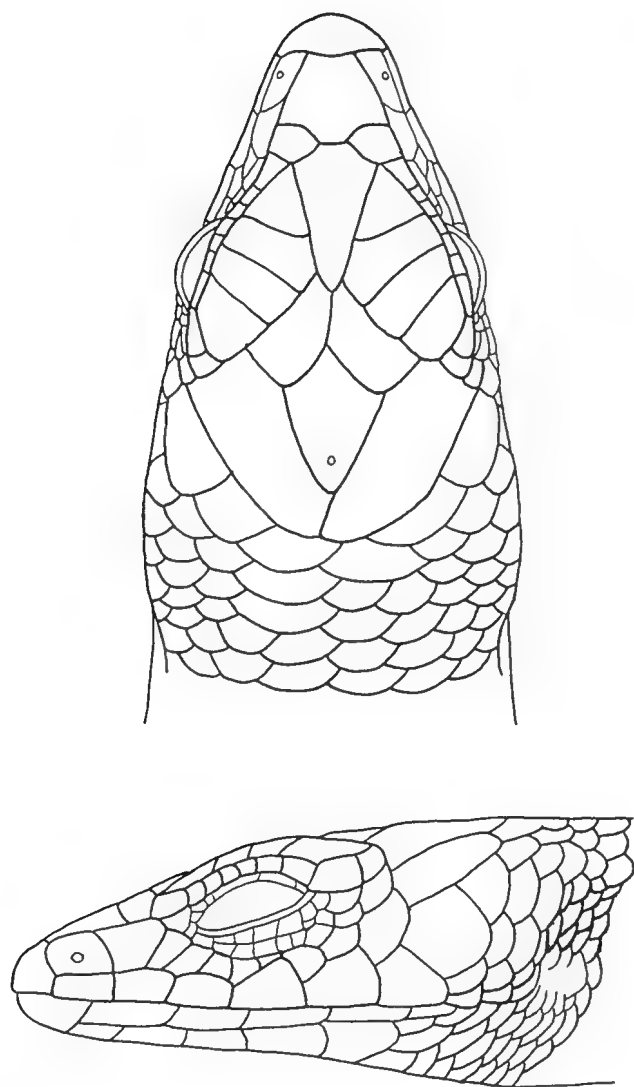


Fig. 13. Dorsal and lateral views of the head of *Calyptotis thorntonensis* (AM R 56574).

length, distalmost scale only single; subdigital lamellae on fourth toe obtusely keeled, 8–10 (\bar{X} = 9.0, mode = 9).

Snout–vent length 29–35 mm; tail length 1.07 times SVL (but N = 1); front leg .16–.19 and rear leg .24–.27 times SVL.

Presacral vertebrae 26; phalangeal formulae for manus and pes 2–3–4–3–3 and 2–3–4–4–4 respectively.

Colour in preservative. Dorsum medium to dark brown with darker mottling very roughly following the scale edges, this pattern more or less conspicuous depending on the intensity of the ground colour. An ill-defined dark dorsolateral stripe extends from the loreal area through the eye and onto the body; this stripe is most distinct on the neck and shoulder. Flanks light brown with dark mottling. Venter off white, immaculate except for dark spotting on the tail and side of chin and throat. First supralabial entirely dark but succeeding supralabials with light central areas.

Colour in life. No specific notes were made on the coloration of the animals in life, but the recollection of those who handled the animals was that there was no colour.

Details of the holotype. The holotype (QM J 28354) is a male with a snout–vent length of 29 mm and a tail length of 35 mm, of which 5 mm is regenerated; supraciliaries 8/8; enlarged nuchals 3/1; midbody scale rows 24; paravertebral scales 53 and subdigital lamellae 8/10.

Etymology. The name *thorntonensis* derives from Thornton Peak, the type and, as yet, only known locality for the species.

Distribution. The species is known only from the type locality on the southern base of Thornton Peak in north-eastern Queensland at an elevation of approximately 640 m (Fig. 14).

This locality lies approximately 600 km north of the nearest population of any other member of *Calyptotis*, i.e. *C. temporalis* at Cathu State Forest.

Habitat. The type locality is site number 39 in the Australian Museum–Queensland Museum joint faunal survey of the fauna in eastern Australian rainforests (Broadbent and Clark, 1976). It is a wet mesophyll vine forest on a rather steep, rock-studded slope. All specimens were found beneath rocks.

The locality was shrouded in low clouds, mist and rain for the two days the collecting party was on the site, and to judge from the accounts of both local residents and members of other expeditions these conditions are not atypical.

The only other reptiles at the site were *Lampropholis basiliscus* and “*Tropidophorus*” *queenslandiae*. Both these species are endemic to the rainforests of north-eastern Queensland.

Behaviour. One of the most remarkable characteristics of *C. thorntonensis* is its sensitivity to heat. I discovered this when a large specimen I was holding gently in my fingertips in cool shade, gradually went limp and only recovered after being placed free on a piece of cool plastic. Dr H.G. Cogger also discovered the species’ sensitivity when specimens began succumbing while being held in plastic bags exposed to shaded ambient midday temperatures at low elevation. The conditions under which these specimens succumbed were both fairly routine, hence the response was especially surprising and noteworthy.

Comparison with other *Calyptotis*. Comparisons between *C. thorntonensis* and *C. ruficauda*, *C. lepidorostrum*, *C. scutirostrum* and *C. temporalis* have been made on pp. 34, 39, 44, and 47, respectively and also in Table 5.

The Intrageneric Relationships of *Calyptotis*

There are ten characters which vary interspecifically in *Calyptotis* and whose phylogenetic polarity can be inferred with some confidence (see characters B, D–H and L–O in the Appendix). These characters provide a

basis for inferring the relationships of the species within the genus and for assessing their degree of divergence from each other and from their hypothetical common ancestor. In this analysis, groups are based on shared derived character states and an effort is made to minimize the number of character state changes linking the taxa in their hypothetical phylogeny (without invoking reversals).

The two most parsimonious hypotheses for the interspecific relationships of *Calyptotis* based on these characters are depicted in Figure 18. The two phylogenies differ only with regard to the placement of *C. temporalis*, and this in turn depends on whether one emphasizes the loss of a single phalange in the fourth (indicating relationship with *C. thorntonensis*) or fifth (relationship with the *C. ruficauda*–*C. lepidorostrum*–*C. scutirostrum* line) toe of the pes. In either case the consequence is the parallel loss of the phalange in the other digit. Both hypotheses are thus equally plausible and to decide between them objectively requires additional characters.

There are two general points in which the phylogenies agree. First, *C. ruficauda* is the most generally primitive species of *Calyptotis*. This species is primitive in all but one of the ten characters analysed, and thus conforms closely to the hypothetical common ancestor of the genus. The primitive character states shown by *C. ruficauda* are as follows: process of posteromedial corner of palatal ramus of pterygoid short and hence posterior notch of ramus correspondingly shallow (b) (Fig. 21); postorbital bone present (D); presacral vertebrae 26 (E); phalanges in manus 2–3–4–4–3 (f); head and body relatively deep (H); prefrontal scales present (L); external ear with a scaleless tympanum (M); secondary temporals two (N); and scales on dorsal surface of toes in multiple longitudinal rows (O). The single derived character state shown by *C. ruficauda* is the loss of a phalange in the fifth toe of the pes (g).

Second, the separation between the *C. ruficauda*–*C. lepidorostrum*–*C. scutirostrum* line and the *C. thorntonensis* line appears to go back to the common ancestor of the genus because each retains a unique primitive character: five phalanges in the fourth toe of the pes in the *C. ruficauda* line and four phalanges in the fifth toe of the pes in the *C. thorntonensis* line.

Third, *C. lepidorostrum* and *C. scutirostrum* are very closely related, the latter probably having evolved morphologically from the former simply through the fusion of the prefrontals and frontonasal.

Finally, it is worth noting that both phylogenies suggest that mosaic, parallel and convergent evolution have all occurred in *Calyptotis*. Mosaic evolution is evident, for example, in the development of the unique secondary temporal scale in *C. temporalis* with its contrastingly primitive postorbital bone, 26 presacral vertebrae, 2–3–4–4–3 phalanges in the manus, deep head and body, and naked tympanum; parallel evolution is evident in the loss of the prefrontal scales in both *C. scutirostrum* and *C. temporalis*, and convergent evolution is evident in the development of the scaly

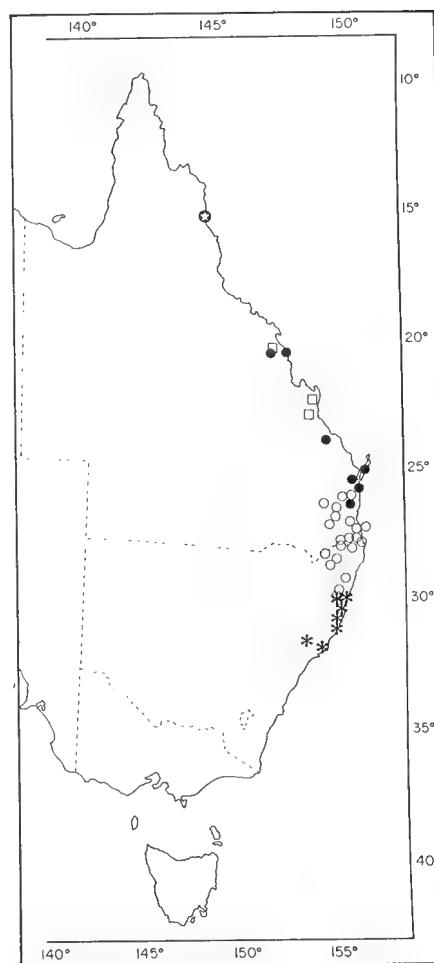


Fig. 14. Map of Australia showing the distribution of the five species of *Calyptotis*: *ruficauda* (asterisks), *scutirostrum* (open circles), *lepidorostrum* (black dots), *temporalis* (open squares) and *thorntonensis* (black dot with open star).

tympanum in both the *C. lepidorostrum*–*C. scutirostrum* line and *C. thorntonensis*.

The Intergeneric Relationships of *Calyptotis*

Within the *Sphenomorphus* group, *Calyptotis* shares the largest number of derived character states with *Saiphos*, a monotypic genus of elongate (maximum SVL = 87 mm) tridactyl skinks which inhabit cool, moist habitats along the coastal lowlands and adjacent mountains from south-eastern Queensland south to the Illawarra area of New South Wales (Figs 15–17). The two genera share five derived character states: palatal rami of pterygoids approximately triangular in shape and separated anteriorly to varying degrees by posteriorly projecting processes from the posteromedial corners of the palatines (a); palatal rami with slight posteriorly projecting processes from their posteromedial corners (b) (Fig. 21); phalanges in fourth toe of the manus four (*Calyptotis*) or fewer (*Saiphos*–3) (f); loreal single (j); and fourth supralabial subocular (k). The two genera also share a relatively low number of longitudinal scale rows at midbody (≤ 24) and a bright



Fig. 15. *Saiphos equalis* (gravid female) from "Tallawong", Mt. Irvine, NSW.

ventral colour which involves some shade of yellow and/or red and extends from the level of the forelegs back, but the phylogenetic significance of these characters is uncertain. The morphological and ecological similarity between the two taxa plus their geographical proximity suggest that they are each other's closest living relatives.

There appear to be two equally plausible hypotheses with regard to the relationship between *Saiphos* and *Calyptotis* (Fig. 18). The first is based on a primitive character state possessed by *Saiphos* but not seen in *Calyptotis*—the postmental in contact with two infralabials (l) instead of (i)—and suggests that the two taxa shared a common ancestor with this primitive feature. The second takes note of the three derived character states shared by *Saiphos* and *Calyptotis scutirostrum*—increased number of presacral vertebrae (e), loss of prefrontals (l) and presence of a scaly auricular depression (m)—and suggests that *Saiphos* was derived from a form like *Calyptotis scutirostrum*. Under the first hypothesis the three derived character states shown between *Saiphos* and *Calyptotis scutirostrum* are interpreted as convergent, and under the second having the two infralabials in contact with the postmental is interpreted as the reacquisition of a primitive character state. Both hypotheses are supported by geography because the relevant taxa for each hypothesis—for the first *C. ruficauda* as the most generally primitive *Calyptotis* and for the second *C. scutirostrum*—are both parapatric with *Saiphos*. Additional characters will be needed to test further these two hypotheses.

It is important to note that even if *Saiphos* is closely related to *Calyptotis scutirostrum* it is still distinguished

from this and other species of *Calyptotis* by a number of unusual or unique derived character states. This makes it useful to continue treating the taxon as a distinct genus. These character states are: posteromedial processes from the palatal rami of the pterygoids extended posteriorly (b') (a similar but less well developed extension occurs in *C. temporalis*); maxilla and frontal bones in superficial contact (c); postorbital bone absent (d) (also in *C. thorntonensis*); presacral vertebrae increased to 38–40 (e'); phalanges reduced to 0–2–3–3–0 in manus (f'') and to 0–2–3–3–0 in pes (g''); and retention of the eggs either to term as in the cooler northern highlands part of its range (Bustard, 1964 and pers. obs.) or to within a few days of term in the southern part of its range (p) (pers. obs.).

If one makes the further assumption that for those characters in which the polarity of states is uncertain the primitive condition is shown by the more generally primitive species in the *C. ruficauda*–*C. scutirostrum* line, then the following character states can also be interpreted as derived in *Saiphos*: body length increased by approximately half (to a maximum of 87 mm from approximately 55 mm); tail length relative to SVL slightly decreased (to a maximum of 1.3 from approximately 1.5); limbs reduced in absolute size; ventral colour uniform with loss or masking of yellow on body; loss of sexual dichromatism in intensity of ventral colour, and relatively small brood size through failure of brood size to increase with body size (Table 6).

It is tempting and perhaps even reasonable to interpret most of the morphological and osteological specializations of *Saiphos vis-à-vis Calyptotis* as adaptations to its more burrowing existence. Certainly

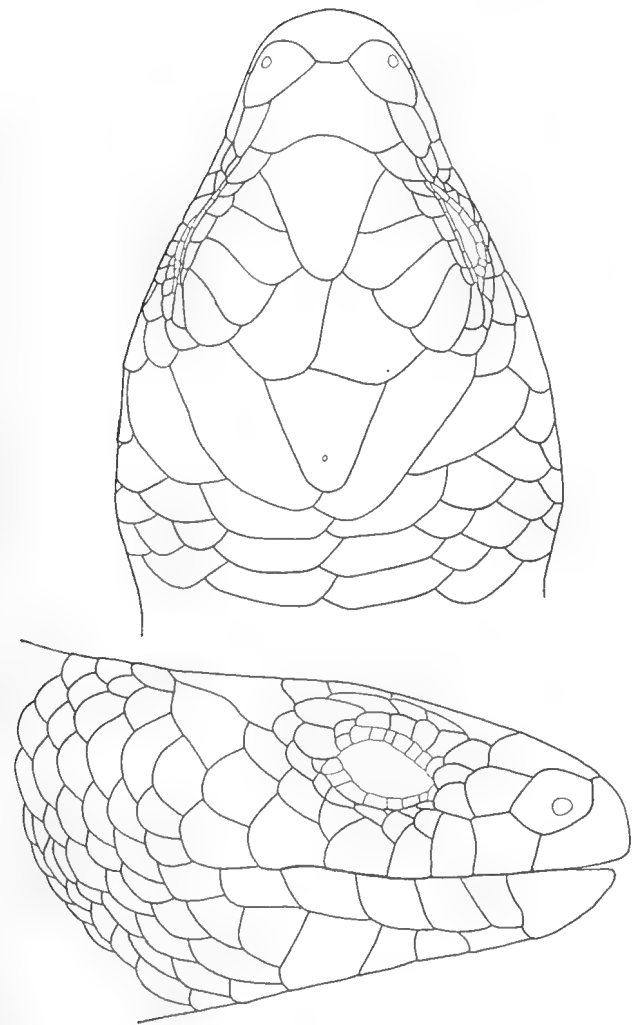


Fig. 16. Dorsal and lateral views of the head of *Saiphos equalis* (AM R 87316).

features such as body elongation, tail shortening (relative to SVL), limb and digit reduction, loss of external ear opening and perhaps loss of the postorbital are plausible burrowing adaptations, as they appear to have evolved in a number of burrowing lineages. The reproductive specializations of *Saiphos*, however, are probably best interpreted as another example of the

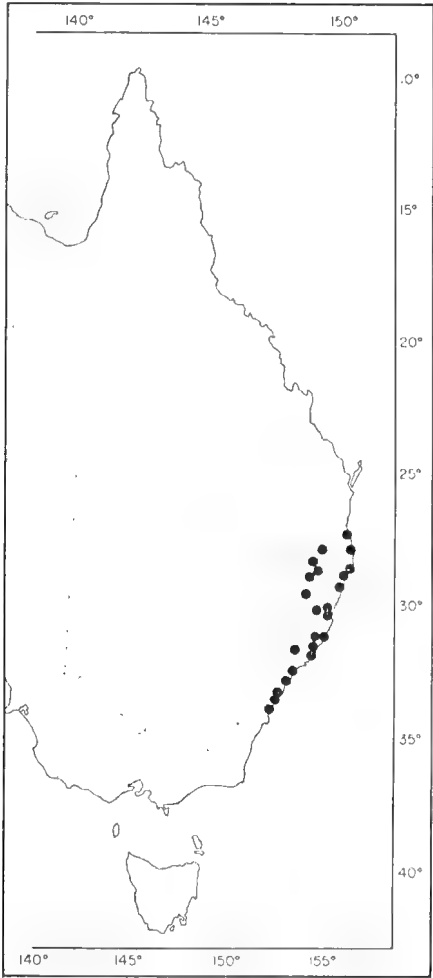


Fig. 17. Map of Australia showing the distribution of *Saiphos equalis*.

evolution of egg retention and live bearing in a cool climate, albeit an especially interesting one in that it involves intraspecific variation. The significance of the loss of the body–tail difference in ventral colour and the loss of sexual dimorphism in the intensity of ventral colour in *Saiphos* is obscure, but may be related to its more cryptozoic habits and presumed attendant loss or reduction of the visual component in intraspecific communication.

Table 6. Summary of information on the size of gravid females and their brood size in four species of *Calyptotis* and *Saiphos equalis*.

	<i>C. ruficauda</i> (N = 10)	<i>C. lepidorostrum</i> (N = 8)	<i>C. scutirostrum</i> (N = 21)	<i>C. temporalis</i> (N = 1)	<i>S. equalis</i> (N = 44)
Size of gravid females (mm)					
Range	42–52	39–55	42–59	36	58–87
Mean	48.5	49.3	48.5		74.7
S.D.	2.99	4.95	5.32		6.58
Brood sizes					
Range	2–6	2–4	1–5	2	1–7
Mean	3.3	3.4	3.2		2.9
S.D.	1.25	.92	.92		1.04

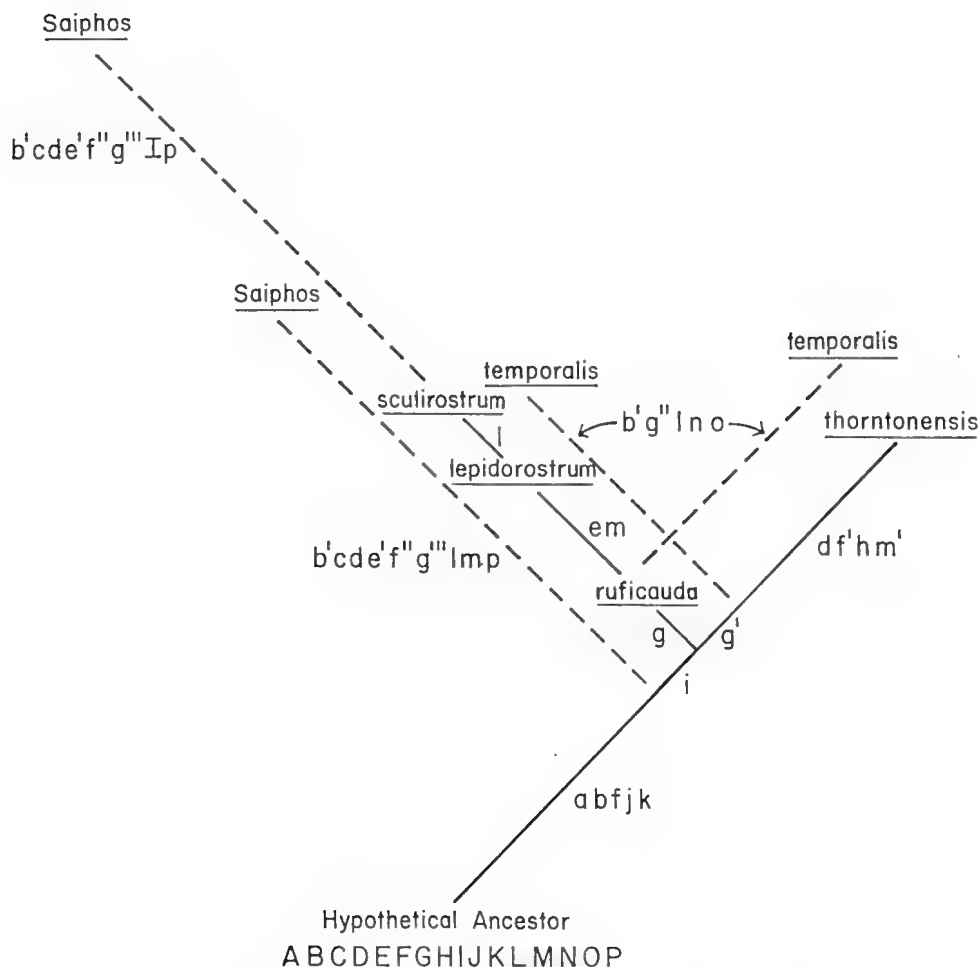


Fig. 18 Summary of the phylogenetic relationships of *Saiphos* and the species of *Calyptotis* as inferred from an analysis of 12 characters (C-E, G-I, L-P, see Appendix). The distance between any two species along the branches of the phylogeny is roughly proportional to the number of character state changes that separate them. The lower case letters beside each section of the phylogeny indicate the character state changes that are hypothesized to have occurred in that part of the phylogeny. Taxa whose relationships are subject to alternative interpretations have those alternatives shown by broken lines.

The Relationships of the *Calyptotis*-*Saiphos* Lineage

It would be interesting to know the closest living relative of the *Calyptotis*-*Saiphos* lineage, if for no other reason than it would allow a more detailed assessment of primitive and derived character states, and hence relationships, within the lineage itself. On the basis of present knowledge this relative would only be recognizable if it shared one or more of the five derived character states that distinguish *Calyptotis* and *Saiphos* as a lineage within the *Sphenomorphus* group (see pp.49 above).

Unfortunately, any search for this relative using these characters is hindered by two problems. First and most serious is an incomplete understanding of the distribution of the character states within the *Sphenomorphus* group. This is especially true of the osteological characters in many of the smaller and rarer species of south-east Asia and the Indo-Australian Archipelago. The second problem is convergence. This

is especially true of the two scale characters—the single loreal and fourth supralabial subocular—both of which appear to be associated with small size. Both problems would be diminished by a more thorough knowledge of the five characters within the *Sphenomorphus*, but the size of the group plus its many rare and undescribed species make it certain that this knowledge will develop only slowly.

ACKNOWLEDGEMENTS. The Queensland National Parks and Wildlife Service issued me with the permits to collect in that state, and the Queensland Forestry Department allowed me to traverse and collect in the forests under their jurisdiction.

Many of the specimens utilized in this study were collected by the staffs of the Australian Museum and the Queensland Museum during the course of a survey of the eastern Australian rainforests. This survey was conducted under a grant from the Interim Council of the Australian Biological Resources Study.

Key to the Species of *Calyptotis*

1. External ear indicated by a shallow auditory meatus and a scaleless tympanum . . 2
 - External ear indicated by a depression that is completely scaled 3
2. Secondary temporals two; prefrontals present; upper surface of digits covered by two or more rows of scales *C. ruficauda*
 - Secondary temporal single, large; prefrontals absent; upper surface of digits covered by a single row of scales *C. temporalis*
3. Head and body relatively deep; ear a scaly, conical depression; postorbital bone present 4
 - Head and body depressed; ear a scaly, superficial disc (tympanum); postorbital absent *C. thorntonensis*
4. Prefrontals present *C. lepidorostrum*
 - Prefrontals usually absent *C. scutirostrum*

Ms Jeanette Covacevich, the Curator of Reptiles in the Queensland Museum, made the specimens in that collection available to me and answered numerous queries for me. Mr Greg Czechura, the assistant in the Department of Reptiles in the Queensland Museum, documented the area of parapatry between *Calyptotis lepidorostrum* and *C. scutirostrum* in the Conondale Ranges in south-eastern Queensland and hence provided the key to the taxonomic interpretation of these two forms. Mr Czechura provided me with extensive accounts of this situation in correspondence and then gave me a guided tour of the area so that I could see it for myself. His extensive knowledge of the Conondales and congenial company in the field are greatly appreciated.

My wife Phylp has once again contributed substantially to the paper with her assistance in the field, editorial comments and art work (Figs 2, 3, 5, 6, 8, 9, 11, 13, 16, 19-22).

The paper has also been greatly helped by having been reviewed critically in various stages by the following people: H.G. Cogger, J. Covacevich, G.V. Czechura, M. Hutchinson, G.J. Ingram and R.G. Zweifel.

Finally, I would like to acknowledge the support of the Australian-American Educational Foundation. It was while I was working under a Fulbright Fellowship from this institution that I originally became interested in the animals discussed here and began the field and laboratory work for this paper.

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Appendix

Phyletic Analysis of Character States

The method for inferring the polarity of character states used in diagnosing taxa and analysing their relationships has been discussed in enough detail elsewhere not to warrant lengthy consideration here (for recent discussions involving reptile examples see Moffat, 1973, Kluge, 1976, and Hecht, 1976). Briefly, the method is based on the assumption that the primitive state of a character that varies within a group is that state that occurs exclusively in the group's nearest relative, or if the character varies within those relatives, in the group's next most closely related relatives.

For the purposes of this analysis the group under consideration is, of course, the *Calyptotis-Saiphos* lineage, and this group's successively more distant relatives are (1) all other members of the *Sphenomorphus* group (p.30)¹; (2) all other lygosomines with special reference to *Mabuya*, the most generally primitive living genus of this subfamily of skinks; (3) all other skinks with special reference to *Eumeces*, the most generally primitive living genus of the family, and (4) all other lepidosaurs with special reference to the Gerrhosauridae, probably the closest living relatives of skinks.

A and B. *Configuration of bones in the posterior part of the secondary palate.* In all lygosomines the palatine bones are roughly rectangular in shape and meet along the midline to form a secondary palate. In the most primitive lygosomines—*Mabuya* and the seemingly most primitive members of the *Sphenomorphus* group—the palatal rami of the pterygoids (which follow the palatines) diverge smoothly from the midline posteriorly and do not contribute substantially to the secondary palate. In several diverse lygosomine lineages, however, the palatal rami meet or approach along the midline in various configurations and thereby extend the secondary palate posteriorly.

In the *Sphenomorphus* group the most common configuration is for the palatal rami to be roughly rectangular or square in shape and to meet broadly along the midline (A). The most plausible explanation for the evolution of this configuration is through the progressive posterior apposition of the medial edges of the rami. Indeed, there is a group of closely related species in *Sphenomorphus* (members of the *variegatus* species group) that can be arranged in just such a morphocline, e.g. *S. indicus* and *S. tersus*—*S. nitidus* and *S. sanctus*—*S. striolatus* and *S. anomalopus*—*S. variegatus*.

In the *Calyptotis-Saiphos* lineage the palatal rami differ somewhat from the derived condition described above, i.e. palatal rami squared off and meeting medially. The rami are basically triangular in shape (i.e. narrow anteriorly and broad posteriorly) and are separated to varying degrees by posteriorly extending processes from the posteromedial corners of the palatines (Fig. 21). Unfortunately the evolution of this configuration is unclear. It could have evolved from the primitive lygosomine condition by the simultaneous medial expansion of the posterior parts of the palatal rami and the posterior extension of the posteromedial processes of the palatines, or it could have evolved from the common *Sphenomorphus* group pattern (A) by the anterior separation of the palatal rami and the posterior extension of the palatine processes (a). I suspect that the latter sequence is correct and assume it to be true for the analysis here. Be that as it may, it is clear that the basic configuration of bones in the posterior part of the secondary palate in the *Calyptotis-Saiphos* lineage is derived within the *Sphenomorphus* group and hence is of importance in diagnosing the lineage within the group.

A second important feature of the *Calyptotis-Saiphos* secondary palate is the process from the posteromedial corner of the palatal ramus (Fig. 21). This process can be viewed as yet a further extension of the secondary palate—probably from a condition in which the rami meet or are apposed at smooth rounded corners (B)—and hence appears to be yet another derived character state (b) that distinguishes *Calyptotis* and *Saiphos* as a lineage within the *Sphenomorphus* group.

The process varies in its degree of development within the lineage. In *Calyptotis ruficauda*, *C. lepidorostrum*, *C. scutirostrum* and *C. thorntonensis* the process is relatively short (b) and probably represents the primitive condition. In *Saiphos* and to a lesser extent *Calyptotis temporalis*, however, the process is somewhat longer (b') and probably represents the derived condition. The similarity between these last two forms has probably resulted from parallel evolution rather than inheritance from a common ancestor because, as the total phylogenetic analysis shows (Fig. 18), it is supported by only one other character (absence of prefrontals) and is not corroborated by geography.

C. Superficial contact between prefrontal, nasal, frontal and maxilla bones. These four bones may form one of two basic configurations on the dorsolateral surface of the snout of adults¹: (1) the sutural contact between the prefrontal and nasal may be exposed due to the separation of the frontal and maxilla or (2) the frontal may contact the maxilla and thereby cover the contact between the prefrontal and nasal. In certain cases all four bones may meet at a point, but this configuration is rarely modal and with a series of adult specimens most species can be assigned unequivocally to one of the two basic configurations.

¹The more closely related phylogenetically the relatives are to the group under study, the more weight they carry in assessing the polarity of character states within the group. For reasons explained in a preceding section, however, it is not yet possible to identify the closest living relatives of the *Calyptotis-Saiphos* lineage. For this reason I have adopted the conservative approach of taking all other members of the *Sphenomorphus* group as the closest relatives of this lineage.

¹Ontogenetic variation makes it mandatory that mature animals be used in evaluating this character.

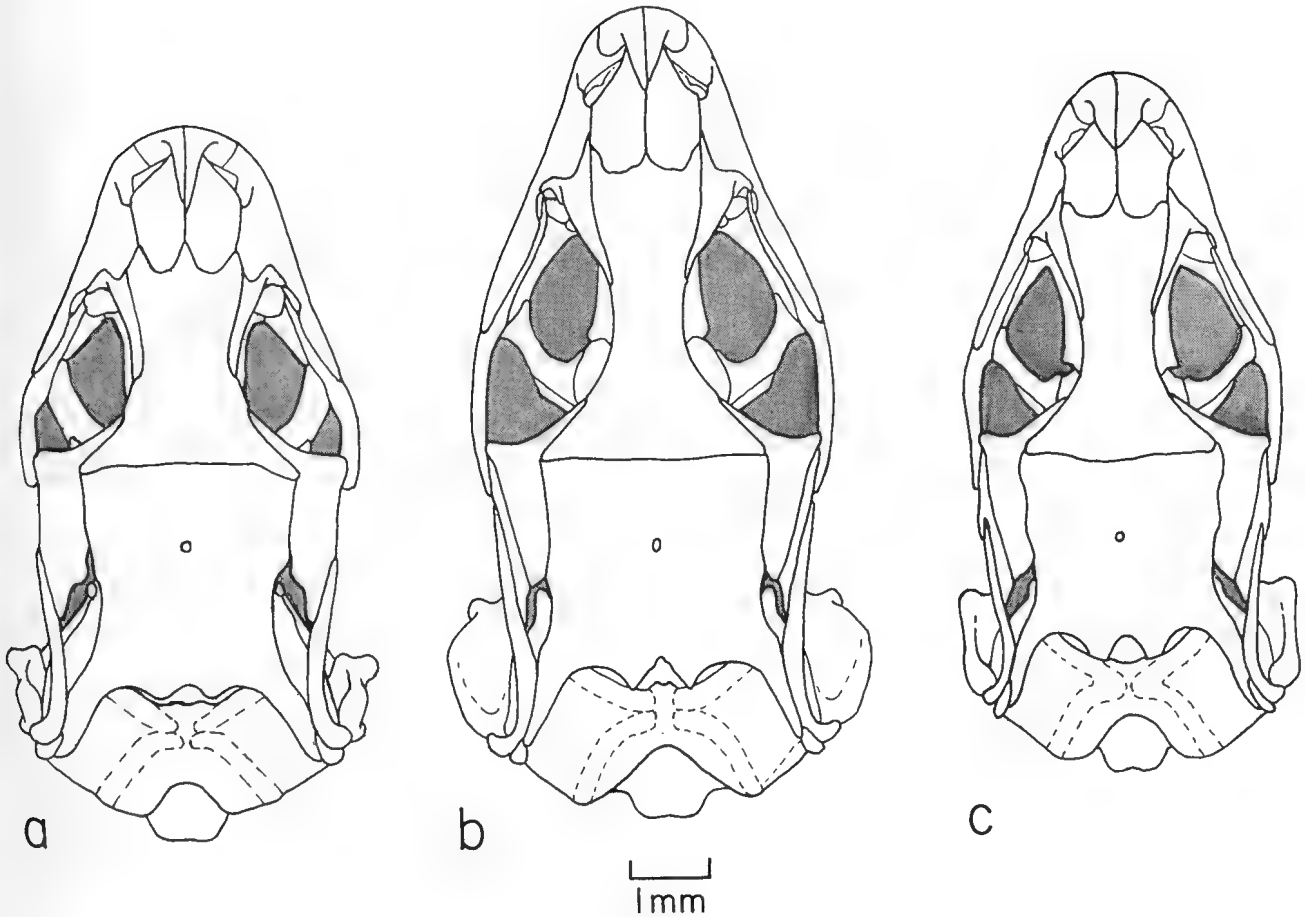


Fig. 19. Dorsal view of the skull of (a) *Saiphos equalis* (AM R 7242); (b) *Calyptotis ruficauda* (AM R 52339), and (c) *Calyptotis scutirostrum* (AM R 43061).

It is difficult to infer the phylogenetic polarity of the two configurations in the *Calyptotis*–*Saiphos* lineage because there are no clear trends in the taxonomic distribution of the character states in the relatives of the group. Most of the taxonomically stable genera in the *Sphenomorphus* group are characterized by one state or the other, but the genera are about evenly divided on this basis. The species within the large and taxonomically ‘unstable’ genus *Sphenomorphus* are also about evenly divided, and the same is true of the species of *Mabuya* (Table 7). Most species of *Eumeces* have the frontal in contact with the maxilla, but many other scincine genera have the prefrontal in contact with the nasal. The closest relatives of skinks—the gerrhosaurids—have the contact between the prefrontal and nasal exposed. This suggests that this condition is primitive for skinks as a group and that unless there is evidence to the contrary it is the condition most logically taken as primitive for any group within skinks. In this analysis, therefore, the superficial exposure of the contact between the prefrontal and nasal is taken as primitive (C) and the covering of this contact by the contact of the frontal and maxilla is taken as derived (c). *Calyptotis* has the contact of the prefrontal and nasal exposed whereas *Saiphos* has this contact covered by

the contact of the frontal and maxilla (Figs 19, 20).

D. Postorbital bone. The postorbital bone occurs in a wide variety of reptiles (Romer, 1956) including gerrhosaurids, and hence its presence in skinks is almost certainly the primitive condition (D) and its absence either through loss or fusion is derived (d).

The postorbital is present in *Calyptotis ruficauda*, *C. lepidorostrum*, *C. scutirostrum* and *C. temporalis* and absent in *C. thornstonensis* and *Saiphos* (Figs 19, 20). When present in *Calyptotis* the bone is long and thin and extends posteriorly to the supratemporal fenestra.

E. Presacral vertebrae. The modal number of presacral vertebrae in those skinks that have not undergone any marked limb reduction is 26 (Hoffstetter & Gasc, 1969); hence this number can be taken as primitive (E) and any deviations from it can be taken as progressive derivations (e).

Calyptotis ruficauda, *C. temporalis* and *C. thornstonensis* have 26 presacral vertebrae (E); *C. lepidorostrum* has 29 (e), *C. scutirostrum* 29–30 (e) and *Saiphos equalis* 38–39 (e') (Table 7).

F–G. Phalanges. The ‘basic’ phalangeal formulae for lepidosaurs are 2–3–4–5–3 (F) for the manus and 2–3–4–5–4 (G) for the pes (Romer, 1956). These formulae also characterize most robust-limbed,

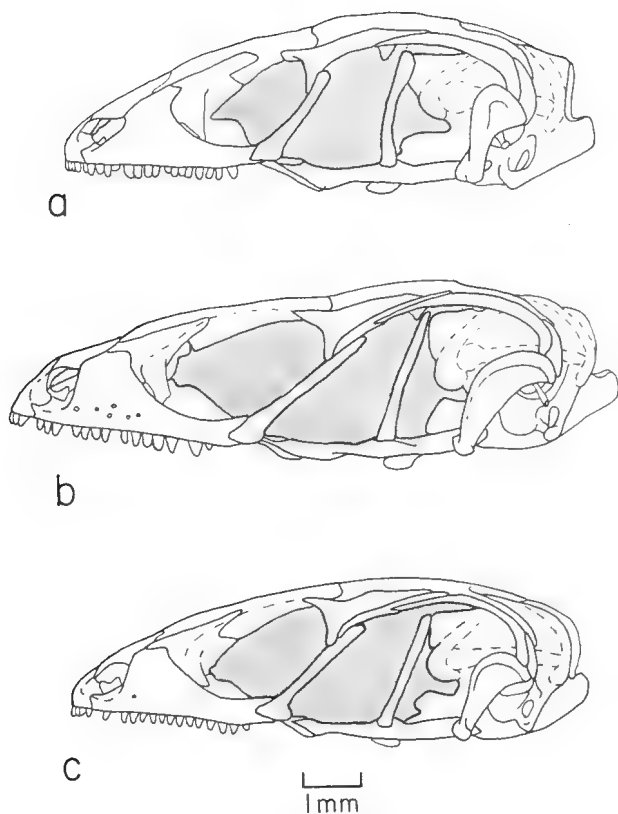


Fig. 20. Lateral view of the skull of (a) *Saiphos equalis*; (b) *Calyptotis ruficauda*, and (c) *Calyptotis scutirostrum*. Same specimens as in Fig. 19.

pentadactyl skinks, including *Eumeces* and *Mabuya*. This suggests that these formulae are primitive for skinks.

For the manus, *Calyptotis ruficauda*, *C. lepidorostrum*, *C. scutirostrum* and *C. temporalis* have a phalangeal formula of 2-3-4-4-3 (f); *C. thorntonensis* has 2-3-4-3-3 (f') and *Saiphos equalis* 0-2-3-3-0 (f'') (Table 7). The formula 2-3-4-4-3 is taken as primitive for the *Calyptotis*-*Saiphos* group because it is closest to the primitive lepidosaur formula (F). The fourth phalange of the fourth toe is assumed to have been lost independently in both *Saiphos* (f→f'') and *Calyptotis thorntonensis* (f→f'). The contrary assumption, namely that the phalange was lost in an exclusive common ancestor of the two forms, seems unlikely in that it is supported by only one other character state (the absence of the postorbital bone) and is not supported by distribution.

For the pes, *Calyptotis ruficauda*, *C. lepidorostrum* and *C. scutirostrum* have a phalangeal formula of 2-3-4-5-3 (g); *C. thorntonensis* has 2-3-4-4-4 (g'), *C. temporalis* 2-3-4-4-3 (g'') and *Saiphos equalis* 0-2-3-3-0 (g''') (Table 7). The formula 2-3-4-5-4 is taken as primitive (G) for the group because this is the most conservative combination that can account for the evolution of the observed formulae without hypothesizing the reacquisition of a phalange. The reason for excluding this latter possibility is that the acquisition of phalanges, at least as evidenced by hyperphalangy above the primitive number of

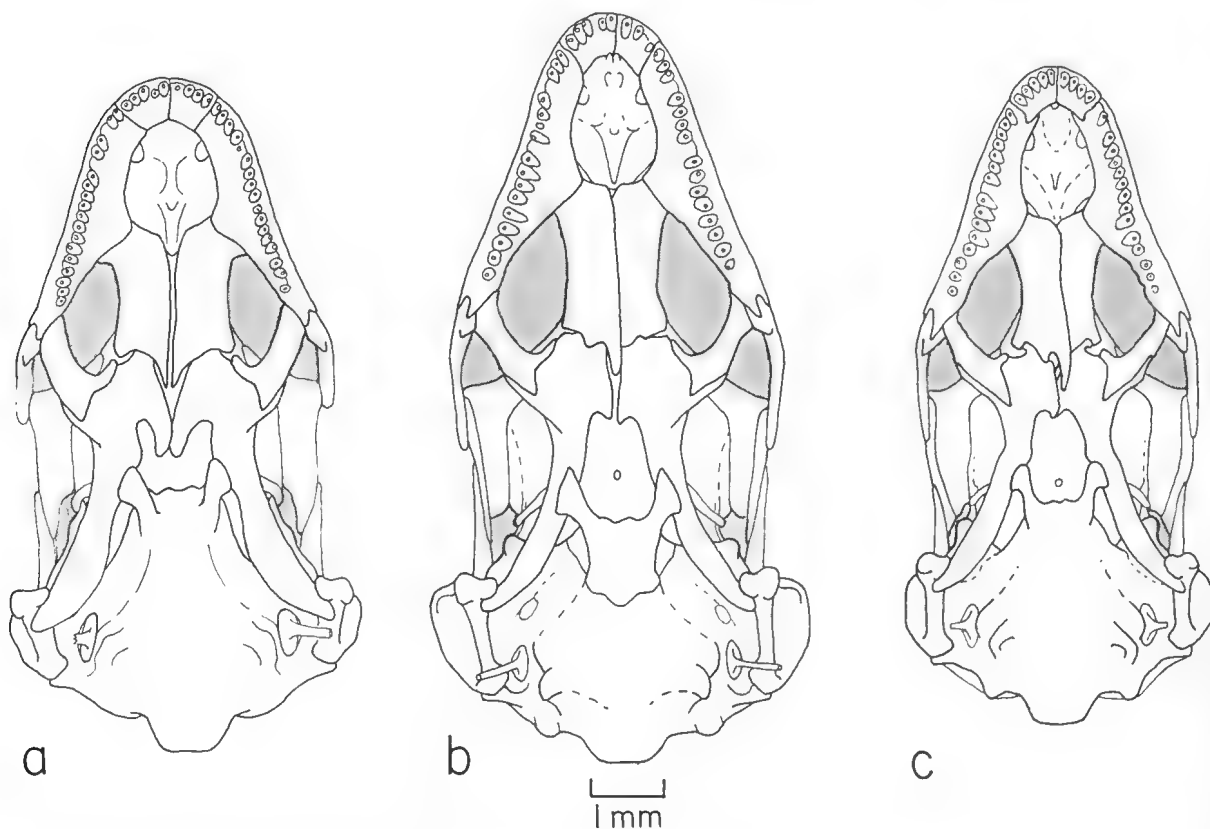


Fig. 21. Ventral view of the skull of (a) *Saiphos equalis*; (b) *Calyptotis ruficauda*, and (c) *Calyptotis scutirostrum*. Same specimens as in Fig. 19.

Table 7. Number of species in *Mabuya* and the genera of the *Sphenomorphus* group showing the prefrontal in contact with the nasal, the frontal in contact with the maxilla, or all four bones in point contact. Species reported here as having a point contact are invariably represented by single specimens. Species with equal numbers of specimens showing the prefrontal in contact with the nasal and the frontal in contact with the maxilla are scored as 0.5 in each of these columns. The total number of species in each genus is given in parentheses.

Taxon	Prefrontal contacts nasal	Frontal contacts maxilla	All four bones in point contact
<i>Mabuya</i> (c.75)	12	12	1
<i>Ablepharus</i> (5)	4	0	0
<i>Anomalopus</i> (12)	2	6	1
<i>Ateuchosaurus</i> (2)	1	0	0
<i>Calyptotis</i> (5)	3	0	0
<i>Ctenotus</i> (c.55)	1	20	0
<i>Eremiascincus</i> (2)	0	2	0
<i>Hemiergis</i> (5)	5	0	0
<i>Isopachys</i> (3)	1	1	1
<i>Lerista</i> (36)	0	9	1
<i>Lipinia</i> (21)	8	0	0
<i>Lobulia</i> (5)	0	2	0
<i>Notoscincus</i> (2)	1	0	0
<i>Prasinohaema</i> (5)	0	3	0
<i>Saiphos</i> (1)	0	1	0
<i>Scincella</i> (c.32)	6	1	0
<i>Tropidophorus</i> (20)	1	4	0
<i>Sphenomorphus</i> (c.180)	21.5	26.5	1

2-3-4-5-4, is extremely rare in skinks (known only in *Scincus* where there is an extra phalange in the fifth digit of both the manus and pes—El Toubi, 1938, and E.N. Arnold, pers. comm.). The loss of phalanges, however, is extremely common in skinks, and especially so in the *Sphenomorphus* group among lygosomines.

H. Depth of head and body. The head and body are relatively deep in the vast majority of skinks and hence this can be taken as the primitive condition (H) in any particular skink lineage. Conversely, a depressed head and body is rare and can be taken as derived (h).

Saiphos and all species of *Calyptotis* except *C. thorntonensis* have a relatively deep head and body. *C. thorntonensis* is noticeably depressed (Fig. 12).

I. Number of infralabial scales contacted by postmental scale. The postmental contacts the first two infralabials in most lygosomines, including the generally primitive genus *Mabuya*, and hence this character state may be taken as primitive (I) in any particular lineage. Conversely, the postmental contacts the first infralabial only in relatively few taxa, for which there is no other evidence of common ancestry, and hence this character state may be taken as derived (i).

Saiphos has the postmental in contact with two infralabials (Fig. 16) but *Calyptotis* with only one (Figs 2, 5, 8, 11 and 13). A comparison of the number of infralabials and the sutural relationships of the labials make it clear that the first two infralabials have fused in *Calyptotis*.

J. Loreal scales. Two loreals, one anterior and one posterior, characterize the vast majority of lygosomine skinks, including the most generally primitive taxa such

as *Mabuya*. This condition, therefore, appears to be primitive (J). A single loreal, in contrast, occurs in relatively few taxa that share little else in common other than perhaps a tendency toward small size. This condition, therefore, appears to be derived (j).

Saiphos and *Calyptotis* both have only a single loreal (Figs 2, 5, 8, 11, 13 and 16).

K. Subocular supralabial scale. The fifth or sixth supralabial is situated below the centre of the eye in most skinks; including *Eumeces* and *Mabuya*. This suggests that one of these scales is primitive for lygosomines (K) and that higher and lower (k) numbers are derived.

Calyptotis and *Saiphos* both have the fourth supralabial subocular (Figs 2, 5, 8, 11, 13 and 16).

L. Prefrontal scales. A single pair of prefrontals occurs in most lygosomine skinks, including all primitive taxa of all major lineages. It would appear, therefore, that the presence of prefrontals is primitive (L) and their absence derived (l).

Prefrontals are present in *Calyptotis ruficauda*, *C. lepidorostrum* and *C. thorntonensis* (Figs 2, 5 and 13) but absent in *C. scutirostrum*, *C. temporalis* and *Saiphos* (Figs 8, 11 and 16).

M. External ear. An external ear comprising a naked tympanum is typical of the more generally primitive skinks such as *Eumeces* and *Mabuya*. This type of external ear, therefore, may be taken as primitive within any skink lineage in which it occurs (M). In contrast, a scaled-over tympanum may be taken as derived (m).

A naked tympanum occurs in *Calyptotis ruficauda* and *C. temporalis* (Figs 2 and 11) and a scaled-over

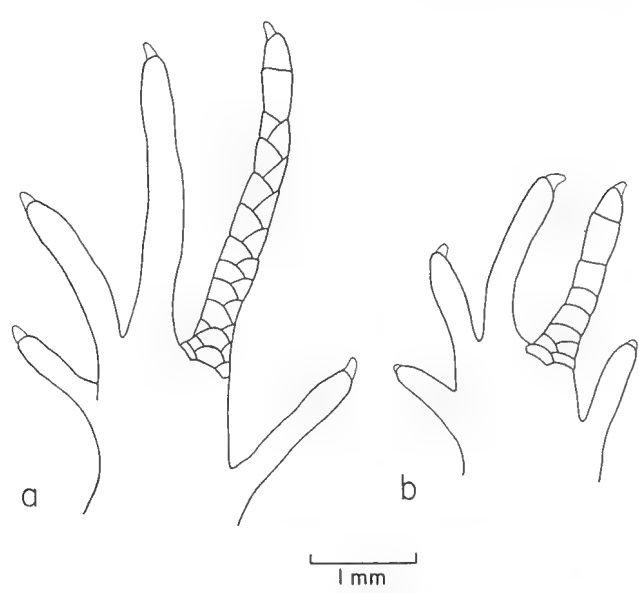


Fig. 22. Dorsal view of the right hind foot of (a) *Calyptotis ruficauda* (AM R 90608) and (b) *C. temporalis* (AM R 60764).

tympanum occurs in *C. lepidorostrum*, *C. scutirostrum*, *C. thorntonensis* and *Saiphos* (Figs 5, 8, 13 and 16). It seems likely, however, that the tympanum may have scaled-over in two different ways in the *Calyptotis*-*Saiphos* group, because in *Calyptotis lepidorostrum*, *C. scutirostrum* and *Saiphos* the scales are relatively small and the underlying dermis thick (m) whereas in *Calyptotis thorntonensis* the scales are larger and the dermis thinner (m').

It may be of interest to note here how little the morphology of the middle ear and its associated structures has changed in the 'earless' forms of the *Calyptotis*-*Saiphos* lineage. The middle ear has been examined in *Calyptotis ruficauda*, which has a distinct external auditory meatus and a scaleless tympanum, and in *C. lepidorostrum*, *C. scutirostrum* and *Saiphos*, which have a scaly conical depression or crease. In all four forms the similarities outweigh the differences. For example, there is always a distinct eustachian tube, middle ear cavity and round window and in all the

columella attaches to the skin at the base of the auricular depression, be it the scaleless tympanum of *Calyptotis ruficauda*, or the scaly depression of the others. The most noticeable difference is in the size of the quadratal conch. In *C. ruficauda*, the conch is fairly well developed and extends along the outer edge of the quadrate for most of its depth; in *C. lepidorostrum* and *C. scutirostrum* the conch is reduced to a small cup-like flange on the dorsal end of the quadrate, and in *Saiphos* it is completely lost and the quadrate is simply a stout vertical shaft.

It would appear therefore that despite the scaling over of the tympanum and the reduction and loss of the quadratal conch, the middle ear in the 'earless' members of the *Calyptotis*-*Saiphos* lineage is still attuned to receiving air-borne vibrations.

N. Secondary temporal scales. Two secondary temporals, one dorsal and one ventral, characterize most skinks. This condition, therefore, may be taken as primitive (N). In contrast, a single temporal is very rare in skinks; therefore, this condition may be taken as derived (n).

Saiphos and all *Calyptotis* except *C. temporalis* have two secondary temporals (Figs 2, 5, 8, 13 and 16). *C. temporalis* has only one (Fig. 11).

O. Scales covering the dorsal surface of the digits. Two or more rows of scales covering the dorsal surface of the digits, especially the fourth toe, appears to be primitive for the *Sphenomorphus* group (O) and a single row derived (o). The basis for this inference has been discussed elsewhere (Greer, 1979).

Saiphos and all *Calyptotis* except *C. temporalis* have two or more rows of scales covering the digits; *C. temporalis* has only a single row (Fig. 22).

P. Mode of reproduction. Oviparity—the laying of shelled eggs which develop to term outside the body of the mother—is almost unquestionably the primitive mode of reproduction for amniotes (P), and ovoviviparity—the deposition of full term young in translucent sacs—is derived (p).

The species of *Calyptotis* for which the mode of reproduction is known (*C. ruficauda*, *C. lepidorostrum* and *C. scutirostrum*) are oviparous. *Saiphos* is nearly

Table 8. Number of presacral vertebrae and phalanges in the species of *Calyptotis* and *Saiphos* as determined by X-ray analysis.

Taxon	Presacral Vertebrae				Phalanges	
	Range	Mean	Mode	N	Manus	Pes
<i>Calyptotis</i>						
<i>ruficauda</i>	26	26	26	10	2-3-4-4-3	2-3-4-5-3
<i>lepidorostrum</i>	29	29	29	9	2-3-4-4-3	2-3-4-5-3
<i>scutirostrum</i>	29-30	29.5	29/30	10	2-3-4-4-3	2-3-4-5-3
<i>temporalis</i>	26	26	26	4	2-3-4-4-3	2-3-4-4-3
<i>thorntonensis</i>	26	26	26	5	2-3-4-3-3	2-3-4-4-4
<i>Saiphos</i>						
<i>equalis</i>	38-40	38.5	38	17	0-2-3-3-0	0-2-3-3-0

or completely ovoviviparous: southern, lowland populations lay a calcium streaked egg which takes 7-8 days to hatch whereas northern highland populations deposit

full term young which break free of their clear embryonic membranes in 1-2 days (Bustard, 1964, and Greer, in prep.).

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Distribution of Teredinids (Mollusca: Teredinidae) in Papua New Guinea

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ABSTRACT. Thirty-eight species of Teredinidae, 2 of which may be new, were collected from the coasts and estuaries of Papua New Guinea. There was little difference in the occurrence of the majority of these species in the Bismarck, Solomon and Coral Seas. A few species restricted to the Bismarck and Solomon Seas have been found in the islands to the north of Papua New Guinea but not in Australia, and one species restricted to the Coral Sea has been previously reported only from north-east Australia.

There was a significant difference in the species composition in estuarine brackish waters compared with that in coastal marine waters. The teredinids may be put into 4 categories according to their occurrence in waters of different salinities: stenohaline marine species, euryhaline marine species, brackish water species and euryhaline brackish water species or marine and brackish water species.

RAYNER, S.M., 1983. Distribution of teredinids (Mollusca: Teredinidae) in Papua New Guinea. Records of the Australian Museum 35(2):61-76.

Species in the family Teredinidae, commonly called shipworms or teredos, are bivalve molluscs adapted to boring into wood. Their elongated bodies extend beyond the posterior margin of the shell valves, enabling them to bore deep within the timber while their siphons maintain contact with the seawater.

Prior to 1947 there was no published literature on the marine wood borers of Papua New Guinea. Schillinglaw and Moore (1947) investigated the Service harbour installations from March to July 1945 for the Scientific Liaison and Information Bureau, a war-time organization. They found that when non-resistant timber piling was used there was a general failure of wharves after twelve months. Generally attack was observed to be faster in estuarine conditions, and the rate of destruction in Port Moresby was seen to be markedly less than on the north coast of New Guinea, possibly due to the slightly lower water temperatures along the Papuan south coast. The greatest damage in the wharves was caused by the teredinids, of which 21 unidentified species in six genera were reported. The pholad *Martesia* was found mainly in the intertidal region while the isopods *Sphaeroma* and *Limnoria* were found to be restricted in distribution and of little importance in the destruction of Service structures.

From 1947 to 1970 the only other available literature relevant to marine borers in Papua New Guinea were

the report by Hartwell and Eddowes (1967) on the natural resistance of 22 indigenous timbers to marine wood borers and the reports by Wight (1969) and Tambllyn (1970) on the resistance of treated timbers to marine wood borer attack.

From August to September 1970 I accompanied Dr R.D. Turner, of the Museum of Comparative Zoology, Harvard University, and Ms J.V. Marshall, a postgraduate student with the School of Zoology, University of New South Wales, on an extensive collecting trip to the major ports of Papua New Guinea. This was part of a combined C.S.I.R.O./U.N.S.W. project on a survey of marine wood borers in Australasian waters. Distribution data obtained during this survey are available in UNSW Project 12-045-15 publication 1970-1972 and are included in this paper.

Methods and Materials

From 1971 to 1975 additional data on the occurrence of teredinids were collected through field collections in mangrove and driftwood, from fixed timbers and by the submersion of a large number of test panels in the major estuarine and marine harbours. (The term "mangrove" as used in this report refers to the roots and trunks of mangrove species such as *Rhizophora stylosa*, *Bruguiera*

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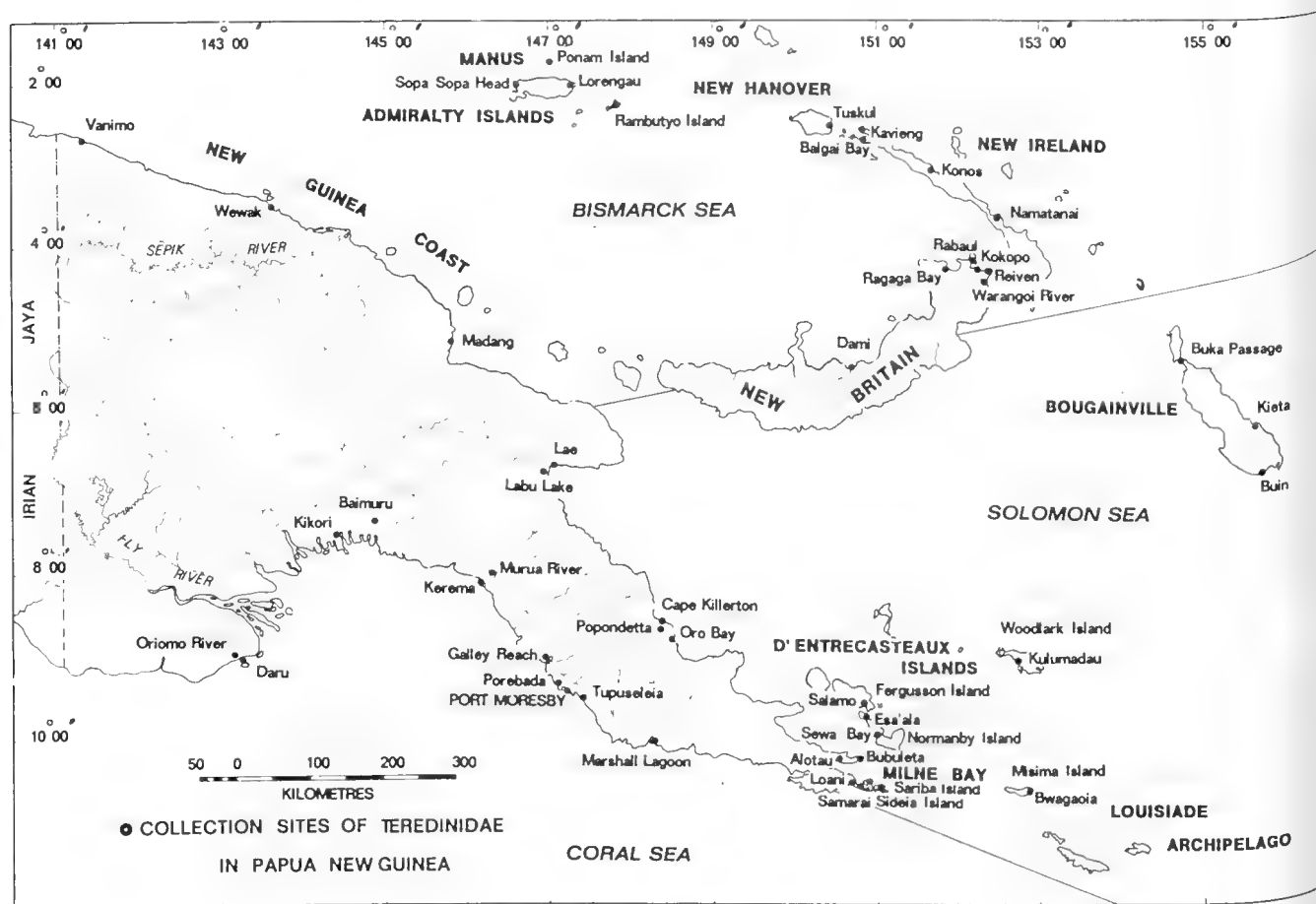


Fig. 1. Collection Sites of Teredinidae in Papua New Guinea.

parviflora, *Xylocarpus granatum*, and *Ceriops decandra* found growing along the coastline and at the mouths of estuaries and the trunks of timber species such as *Pterocarpus indicus*, *Hibiscus tiliaceus* and *Heritiera littoralis* which are found growing along the banks in the upper tidal reaches of rivers. "Fixed timber" refers to test panels, 7.5 x 2.5 x 25.4 cm and mostly of *Intsia bijuga*, preserved test panels and timber structures such as the fenders and piles of old wharves and jetties.) Collecting sites are shown on the map (Fig. 1).

As many whole specimens as possible were manually dissected with Stanley hand-knives from the wood samples. When teredinid attack was very heavy or when the borers had already died and decomposed at the time of the wood's collection only the hard calcareous pallets, which are used to seal off the burrow openings, could be extracted. The borers could still be determined, as identification of teredinid species is almost entirely based on the pallets. I identified each specimen as schooled by Dr Turner during her visit to Papua New Guinea in 1970, in accordance with her key to the wood-boring bivalves (1971). All specimens, preserved in 75% ethanol, are presently held at Forest Products Research Centre, Office of Forests. The Teredinidae collection will be lodged in the Mollusca collection at the Papua New Guinea National Museum in the event of the marine wood-borer programme terminating at the Office of Forests.

Results

Of the 67 species of Teredinidae recognized by Turner (1971), 34 have been collected from the coasts and estuaries of mainland Papua New Guinea, New Ireland, New Britain, the Admiralty Islands, Bougainville Islands, the D'Entrecasteaux Islands and the Louisiade Archipelago (Fig. 1). Two possible new species were found in 1970 by Turner, Marshall and Rayner, one a *Lyrodus*, the other a *Nausitora*. *Lyrodus tristis* Iredale (1936), which had been synonymized with *L. pedicellatus*, and *Nausitora globosa* Sivickis (1928), which had been synonymized with *N. dunlopei* by Turner (1966), are now considered valid species (Turner, pers. comm.). A list of all Teredinidae collected in Papua New Guinea is given in Appendix I, detailing their distribution within the Bismarck, Solomon and Coral Seas.

Discussion

The majority of species range throughout all three seas, a reflection of the uniformity of water temperatures and of the effectiveness of the coastal surface currents, which are important in the dispersal of the adults in driftwood, and of the free-swimming larvae of oviparous and short-term larviparous species. These currents pass through the Vitiaz Straits from the Solomon Sea to the Bismarck Sea from April to October

and from the Solomon Sea to the Coral Sea from June to October during the south-easterly 'trade' winds. From November to March, when the winds are from a westerly direction, surface currents pass through the Vitiaz Straits from the Bismarck Sea to the Solomon Sea, with some current movement from the Solomon Sea to Coral Sea. During this season circular currents in the Coral Sea could allow for the intermixing of teredinid populations in north-east Australia and Papua (Wyrski, 1960, and Yamanaka, 1973). The native canoes used in long trading voyages are not dependent on surface currents and may have been important in the transportation of brackish water species from estuary to estuary, but this has not been documented.

A few species appear to have a restricted range and their distribution here is considered in relation to their known distribution in other waters. Only two species were found restricted to the Coral Sea, *Bankia campanellata*, a tropical world-wide species which is not important in the teredinid fauna here, and *Teredo poculifer*, a brackish water species previously reported only from the rivers of north-east Australia. Only one small population of *Teredo poculifer* was found in the Gonema River during an intensive three year study of the Teredinidae in the Marshall Lagoon Estuary. Intensive sampling in other estuaries may show *Teredo poculifer* to have a wider distribution. The two other species found in Papua New Guinea which have been reported previously only from Australia, *Bankia australis* and *Lyrodus tristi*, have been found in very small numbers in the Bismarck and Solomon Seas.

There are several species localized or in high concentrations in the waters of the Bismarck and Solomon Seas. Of these *Spathoteredo obtusa*, *Bankia johnsoni*, *Bankia philippinensis* and *Bankia bipennata* have been reported from the Philippines and the Malayan Peninsula but not Australia. *Nausitora hedleyi* and *Teredothyra smithii*, also known from the Philippines but not Australia, occur in all three Seas.

Teredo somersi and *Teredothyra dominicensis*, found in very small numbers, mainly in the Bismarck Sea, have previously been recorded from the Atlantic Ocean. They are probably a recent introduction and it is possible they could extend their range in the tropical and sub-tropical waters of the Indo-Pacific.

The five other species which are localized in the Bismarck and Solomon Seas are comparatively rare, but two of these are worth mentioning: a possible new *Nausitora* collected in the Huon Gulf near Lae and at Wewak, and *Bankia australis* previously reported only in the temperate to sub-tropical waters of Australia and New Zealand. *Bankia australis* was collected from *Pinus radiata* panels in Rabaul in 1970 and Turner (1971a) suggests that it could have been introduced during World War II and have survived, becoming part of the teredinid fauna there.

Small numbers of *B. australis* were collected in panels from Madang and Vanimo in 1970 and a few specimens were collected in driftwood at Cape Killerton, Sideia Island, and in mangrove at the mouth of a small estuary

at Kieta. *Bankia australis* has probably been introduced several times but undetermined environmental factors prevent the permanent establishment of this temperate sub-tropical species in the tropical waters here.

Three species (*Teredo bartschi* = (*fragilis*), *Teredo triangularis* and *Lyrodus medilobatus*) occurring in the tropical and sub-tropical waters of Australia and the Philippines have not yet been collected. All three could be expected to occur in Papua New Guinea waters.

There was a significant difference in the species composition of populations in estuarine brackish waters compared with coastal marine waters. Although small populations of marine species have been found in slightly brackish waters (20 to 30‰) only eight marine species are truly euryhaline and are commonly found in the mouths of estuaries, where they must tolerate salinities as low as 10‰ for long periods of time. These more tolerant species are *Lyrodus pedicellatus*, *Lyrodus bipartitus*, *Teredo furcifera*, *Nototeredo edax*, *Bankia gracilis*, *Bankia rochi*, *Bactronophorus thoracites* and *Dicyathifer manni*. Turner (1971) classified *Dicyathifer manni* as a marine and brackish water species, a category in which I feel *Bactronophorus thoracites*, *Bankia gracilis* and *Bankia rochi* should also be included, as these species are commonly found upstream to where the salinity is constantly as low as 10‰, as well as occurring in the marine waters along the coastline. *Dicyathifer manni* and *B. thoracites* are essentially found only in the mangrove stands growing along the coastlines and in the estuaries of Papua New Guinea. *Bactronophorus thoracites* has been found up to 52.6 cm in length by 2.0 cm in diameter, extending up the trunk and down the roots from the intertidal region where they settle. Only two very small specimens have been found in timber, one in a test panel tied to mangrove roots at Marshall Lagoon and one in a boat keel which had been moored alongside mangrove. *Dicyathifer manni* occasionally bores into timber structures occurring near mangrove but these specimens are much smaller than those in mangrove (34.7 x 0.9 cm maximum in mangrove compared with 18.6 x 0.9 cm maximum in timber).

Of the brackish water species, *Teredo poculifer* has only been found in estuarine waters and *Nausitora dunlopei* and *Nausitora globosa* are almost exclusively found in estuarine waters, with isolated specimens occasionally found in marine waters. *Nausitora hedleyi*, classified by Turner (1971) as a marine species, is included here as a brackish water species as it is also found almost exclusively in estuaries.

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Appendix I

List of all Terebinthidae collected in Papua New Guinea

Coll = number of collections made at that site
Spec = number of specimens collected at that site

		Fixed Timber		Mangrove		Driftwood	
		Coll	Spec	Coll	Spec	Coll	Spec
<i>Bactronophorus thoracites</i> (Gould) 1856 (marine and brackish water)							
BISMARCK SEA:	Balgai Bay, River, New Ireland			1	2		
SOLOMON SEA:	Labu Lakes, Lae			1	5		
	Salamo, Fergusson I.			1	2		
	Buka Passage, Bougainville I.			1	5		
	Ieta River, Buka, Bougainville I.			2	4		
CORAL SEA:	Paili Inlet, Marshall Lagoon			1	1		
	Gonema River (4 sites), Marshall Lag.	1	1	8	16		
	McFarlane Harbour, Marshall Lag.			1	4		
	Bootless Bay, East Port Moresby			2	2		
	Pari Village, Port Moresby			1	1		
	Napa Napa, Port Moresby Harbour					1	1
	Hourata Bay, Port Moresby Harbour			1	5		
	Coglan Head, Fairfax Harbour			6	22		
	Fairfax Harbour, Port Moresby			3	14		
	Idler's Bay, West Port Moresby			1	1		
	Laloki River, mouth, Galley Reach			1	23		
	Galley Reach, upstream			1	4		
	Petoi, Kerema Bay			1	15		
	Murua River, Kerema Bay			1	9		
	Mariapepia, Baimuru, Pie River			1	38		
	Pie River, Gulf District			3	17		
	Bristow I., West Papua			1	1		
	Bristow I., estuary, West Papua			1	2		
	Oriomo River, mouth, West Papua			1	4		

		Fixed Timber		Mangrove		Driftwood	
		Coll	Spec	Coll	Spec	Coll	Spec
<i>Dicyathifer manni</i> (Wright) 1866 (marine and brackish water)							
BISMARCK SEA:	Lorengau, estuary, Manus I.			1	6		
	Balgai Bay, estuary, New Ireland			1	1		
	Rabaul, New Britain	1	1				
	Wewak, estuary, Sepik			1	4		
	Wewak, beach, Sepik	1	1				
SOLOMON SEA:	Lake Labu, estuary, Lae			1	1		
	Salamo, Fergusson I.			1	3		
	Sewa Bay, Normanby I.			1	27		
	Kulumadau, Woodlark I.			2	33		
	Bubuleta, NE Milne Bay			2	27		
	Buka, estuary, Bougainville I.			1	8		
	Buka, coast, Bougainville I.			1	8		
	Sideia C.M., Sideia I., Milne Bay					1	1
CORAL SEA:	Kupiano Wharf, McFarlane Harbour	4	8				
	NE McFarlane Harbour, Marshall Lagoon			1	24		
	SW McFarlane Harbour, Marshall Lag.	15	148	4	34		
	Paili Inlet, Marshall Lag.			1	8		
	Wanigela Village, Marshall Lag.	6	34				
	Gonema River (3 sites), Marshall Lag.	7	65	4	22		
	Tupuseleia, Port Moresby			1	7		
	Bootless Bay, Port Moresby			6	281		
	Motupore I., Bootless Bay, Port Moresby			1	1		
	Coglan Head, Port Moresby Harbour			19	283		
	Kanudi, Port Moresby Harbour			3	29		
	Hourata Bay, Port Moresby Harbour			2	36		
	Fairfax Harbour, Port Moresby			5	104		
	Idler's Bay, Port Moresby			3	22		
	Boera, Port Moresby			1	7		
	Lealea, estuary, Port Moresby			1	8		
	Porebada, Port Moresby			1	1		
	Laloki River, mouth, Galley Reach			1	1		
	Galley Reach, upstream			1	2		
	Petoi, estuary, Kerema Bay			1	3		
	Oriomo River, mouth, West Papua	1	3	1	2		
	Bristow I., estuary, West Papua			1	2		
	Bristow I., coast, West Papua			1	1		
<i>Teredothyra smithii</i> (Bartsch) 1927 (marine)							
BISMARCK SEA:	Rabaul, New Britain			1	1		
CORAL SEA:	Napa Napa, Port Moresby Harbour	1	2				
<i>Teredothyra matocotana</i> (Bartsch) 1927 (marine)							
BISMARCK SEA:	Rabaul, New Britain	3	4				
	Pila Pila Beach, Rabaul					1	1
SOLOMON SEA:	Lae, main wharf, Huon Gulf	2	3				
	Cape Killerton, Morobe Coast					1	1
CORAL SEA:	Paili Inlet, Marshall Lag.			1	1		
	Wanigela Village, Marshall Lag.	1	3				

		Fixed Timber		Mangrove		Driftwood	
		Coll	Spec	Coll	Spec	Coll	Spec
<i>Teredothyra dominicensis</i> (Bartsch) 1921 (marine)							
BISMARCK SEA:	Rabaul, New Britain	7	8				
SOLOMON SEA:	Lae, main wharf, Huon Gulf	4	10				
CORAL SEA:	Alotau, Milne Bay	2	6				
<i>Teredothyra excavata</i> (Jeffreys) 1860 (marine)							
BISMARCK SEA:	Rabaul, New Britain	1	1				
SOLOMON SEA:	Lae, main wharf, Huon Gulf	2	2				
<i>Teredora princesae</i> (Sivickis) 1928 (marine)							
BISMARCK SEA:	Ponam I., Admiralty Is					1	10
	Madang Harbour, New Guinea coast	1	1				
<i>Uperotus rehderi</i> (Nair) 1956 (marine)							
BISMARCK SEA:	Ponam I., Admiralty Is					1	1
<i>Uperotus clavus</i> (Gmelin) 1791 (marine)							
CORAL SEA:	Idler's Bay, Port Moresby					1	20
<i>Lyrodus pedicellatus</i> (Quatrefages) 1849 (euryhaline marine)							
BISMARCK SEA:	Lorengau, Manus I., Admiralty Is	6	65				
	Lorengau, river, Manus I.	1	16				
	Langendrowa Village, Rambuyto I.			1	1		
	SW Rambuyto I., Admiralty Is					1	3
	Namatanai, New Ireland	1	2				
	Tuskul, New Hanover, New Ireland	2	13				
	Rabaul, wharf, New Britain	14	1321				
	Vulcan Point, Simpson's Harbour			1	1		
	Dami, West New Britain	3	11				
	Ragaga Bay, New Britain	2	76				
	Warangoi River, NE, New Britain					1	1
	Reivan, NE Britain					1	2
	Madang, wharf, New Guinea coast	14	250		1	2	
	Madang, beach, New Guinea coast					1	2
	Vanimo, New Guinea coast	3	8				
SOLOMON SEA:	Lae, main wharf, Huon Gulf	3	3				
	Oro Bay, Morobe coast	3	101				
	Alotau, Milne Bay	2	6				
	Esa'ala, Normanby I.	3	7				
	Sewa Bay, Normanby I.			1	30	1	6
	Bwagaioia, Misima I.	3	42				
	Buka Passage, Bougainville I.	6	50				
	Kangu Beach, Buin, Bougainville I.	2	19				
	Sideia C.M., Sideia I. East Papua					1	1

		Fixed Timber		Mangrove		Driftwood	
		Coll	Spec	Coll	Spec	Coll	Spec
CORAL SEA:	Kupiano Wharf, McFarlane Harbour	12	40				
	SW McFarlane Harbour, Marshall Lag.	5	24				
	Wanigela Village, Marshall Lag.	5	20				
	Gonema River (3 sites), Marshall Lag.	5	12				
	Motupore I., Bootless Bay			1	4		
	Ela Beach, Port Moresby					1	2
	Port Moresby, wharf	20	291				
	Napa Napa, Port Moresby Harbour	8	39				
	Coglan Head, Port Moresby Harbour			4	27		
	Port Moresby Harbour	4	22				
	Fairfax Harbour, Port Moresby			2	3		
	Roku Bay, Port Moresby			1	2		

Lyrodus bipartitus (Jeffreys) 1860
(euryhaline marine)

BISMARCK SEA:	Lorengau, wharf, Manus I.	5	31				
	Lorengau, river, Manus I.	1	3				
	Namatanai, New Ireland	1	3				
	Rabaul, New Britain	6	10				
	Ragaga Bay, New Britain	2	7				
	Dami, West New Britain	1	2				
	Madang, wharf, New Guinea coast	8	24				
	Madang, beach, New Guinea coast					1	2
	Vanimo, New Guinea coast	2	3				
SOLOMON SEA:	Lae, wharf, Huon Gulf	6	10				
	Oro Bay, Morobe coast	1	10				
	Beama River, mouth, Oro Bay	1	5				
	Sewa Bay, Normanby I.					1	3
	Buka Passage, Bougainville I.	2	2				
CORAL SEA:	Kupiano Wharf, McFarlane Harbour	8	19				
	SW McFarlane Harbour, Marshall Lag.	8	59	1	1		
	Gonema River (2 sites), Marshall Lag.	5	32				
	Wanigela Village, Marshall Lag.	1	1				
	Tupuseleia, Port Moresby			1	1		
	Bootless Bay, Port Moresby			4	25		
	Port Moresby, main wharf	2	26				
	Coglan Head, Port Moresby Harbour			8	28		
	Fairfax Harbour, Port Moresby			1	5		
	Hourata Bay, Port Moresby Harbour			1	6		
	Roku Bay, Port Moresby			1	1		
	Lealea, Port Moresby			1	1		
	Kerema Bay, wharf, Gulf	1	1				

Lyrodus tristi (Iredale) 1936
(marine)

BISMARCK SEA:	Madang, wharf, New Guinea coast	1	1				
	Vanimo, wharf, New Guinea	1	2				
SOLOMON SEA:	Oro Bay, Morobe coast	3	11				

Lyrodus n.sp.
(undescribed, marine)

BISMARCK SEA:	Lorengau, Manus I. Admiralty Is	6	41				
	Tuskul, New Hanover, New Ireland	1	1				
	Rabaul, New Britain	7	20				
	Ragaga Bay, New Britain	3	21				
	Madang wharf, New Guinea coast	8	28				

		Fixed Timber		Mangrove		Driftwood	
		Coll	Spec	Coll	Spec	Coll	Spec
SOLOMON SEA:	Oro Bay, Popondetta coast	2	3				
	Alotau, Milne Bay	3	20				
	Sewa Bay, Normanby I.					1	1
	Buka Passage, Bougainville I.	1	1				
CORAL SEA:	NE McFarlane Harbour, Marshall Lag.			1	1		
	Kupiano wharf, McFarlane Harbour	2	2				
	Wanigela Village, Marshall Lag.	2	2				
	Pari Village, Port Moresby			1	4		
	Port Moresby, wharf	19	62				
	Napa Napa, Port Moresby Harbour	6	10				
	Kerema Bay, estuary, Gulf	6	29				
	Daru, main wharf, West Papua	4	97				

Lyrodus massa (Lamy) 1923
(marine)

BISMARCK SEA:	Sietche Bay, NW Manus I.			1	1		
	Lorengau, wharf, Manus I.	1	1				
	Tuskul, wharf, New Hanover	2	10				
	Namatanai, New Ireland	1	1				
	Rabaul, New Britain	3	4				
	Ragaga Bay, New Britain	1	7				
	Madang, wharf, New Guinea coast	4	7				
SOLOMON SEA:	Lae, Huon Gulf	2	2				
	Alotau, Milne Bay	1	1				
	Esa'ala, wharf, Normanby I.	2	2				
	Sewa Bay, Normanby I.			1	2		
	Sideia I. East Papua					1	14
	Buka Passage, Bougainville I.	2	6				
CORAL SEA:	Tupuseleia, Port Moresby			1	1		
	Bootless Bay, Port Moresby			3	6		
	Pari Village, Port Moresby			3	21		
	Port Moresby, wharf	23	104				
	Kanudi, Port Moresby Harbour			2	7		
	Napa Napa, Port Moresby Harbour	7	33				
	Coglan Head, Port Moresby Harbour			11	180		
	Fairfax Harbour, Port Moresby			2	27		
	Hourata Bay, Port Moresby Harbour			1	16		
	Roku, Port Moresby			1	11		
	Idler's Bay, Port Moresby			3	18		
	Boera, Port Moresby			1	1		
	Lealea, west Port Moresby			1	2		

Teredo furcifera (von Martens) 1894
(euryhaline marine)

BISMARCK SEA:	Lorengau, Manus I.	2	4				
	Langendrowa Passage, Rambuyto I.					1	36
	SW Rambuyto I., Admiralty Is			1	5		
	Langendrowa Village, Rambuyto I.			1	2		
	Tuskul, New Hanover, New Ireland	3	27				
	Rabaul, wharf, New Britain	10	659				
	Ragaga Bay, New Britain	3	21				
	Dami, West New Britain	2	8				
	Madang, wharf, New Guinea coast	15	124			1	1
	Madang, beach, New Guinea coast			1	3		
	Vanimo, West Sepik	3	9				

		Fixed Timber		Mangrove		Driftwood	
		Coll	Spec	Coll	Spec	Coll	Spec
SOLOMON SEA:	Oro Bay, Morobe coast	3	21				
	Alotau, Milne Bay	2	4			1	1
	Esa'ala, Normanby I.	3	136				
	Bwagaoia, Misima I.	2	2				
	Buka Passage, Bougainville I.	7	38				
	Pok Pok I., Bougainville I.			1	1		
	Sideia I., Milne Bay					1	4
	Sariba I., Milne Bay	1	1				
CORAL SEA:	Kupiano wharf, McFarlane Harbour	20	406				
	SW McFarlane Harbour, Marshall Lag.	9	45	2	17		
	Wanigela Village, Marshall Lag.	7	51				
	Gonema River (2 sites), Marshall Lag.	2	12				
	Port Moresby, wharf	28	1151				
	Napa Napa, Port Moresby Harbour	1	6				
	Hourata Bay, Port Moresby Harbour			1	1		
	Coglan Head, Port Moresby Harbour			1	1		
	Kanudi, Port Moresby Harbour			1	1		
	Kerema Bay, Gulf	10	153				
	Daru I., West Papua	2	9				
<i>Teredo clappi</i> (Bartsch) 1923							
(marine)							
BISMARCK SEA:	Langendrowa Village, Rambuyto I.			1	3		
	Tuskul, wharf, New Hanover	2	5				
	Madang, wharf, New Guinea coast	4	4				
SOLOMON SEA:	Buka Passage, Bougainville I.	2	2				
	Sideia I., East Papua					1	4
CORAL SEA:	Kupiano Wharf, McFarlane Harbour	1	1				
	Bootless Bay, Port Moresby			2	3		
	Port Moresby, Wharf	26	183				
	Port Moresby Harbour	1	2				
	Coglan Head, Port Moresby Harbour			2	10		
<i>Teredo mindanensis</i> (Bartsch) 1923							
(marine)							
BISMARCK SEA:	Langendrowa Village, Rambuyto I.					1	4
	Langendrowa Passage, Rambuyto I.			1	2		
	Rabaul, New Britain	11	39				
	Dami, West New Britain	1	4				
	Ragaga Bay, New Britain	2	7				
	Madang, wharf, New Guinea coast	1	1				
SOLOMON SEA:	Lae, wharf, Huon Gulf	3	8				
	Bubuleta, NE Milne Bay			1	2		
	Bwagaoia, wharf, Misima I.	1	1				
	Buka Passage, Bougainville I.	2	2				
	Sideia I. Milne Bay					1	2
CORAL SEA:	Bootless Bay, Port Moresby			3	8		
	Motupore I., Bootless Bay			1	11		
	Port Moresby, main wharf	7	18				
	Coglan Head, Port Moresby Harbour			13	91		
	Hourata Bay, Port Moresby Harbour			1	20		
	Kanudi, Port Moresby Harbour			2	7		
	Fairfax Harbour, Port Moresby			4	36		
	Idler's Bay, Port Moresby			1	1		
	Roku Bay, Port Moresby			1	5		
	Boera, Port Moresby			1	1		
	Porebada, Port Moresby			1	15		
	Daru, wharf, West Papua	1	2				

		Fixed Timber		Mangrove		Driftwood	
		Coll	Spec	Coll	Spec	Coll	Spec
<i>Teredo johnsoni</i> (Clapp) 1924 (marine)							
BISMARCK SEA:	Lorengau, Manus I.	5	115				
	Langendrowa Passage, Rambuyto I.					1	1
	Rabaul, New Britain	8	23				
	Ragaga Bay, New Britain	3	29				
	Dami, West New Britain	1	3				
	Madang, wharf, New Guinea coast	8	21				
	Vanimo, New Guinea coast	2	4				
SOLOMON SEA:	Oro Bay, Morobe coast	1	2				
	Alotau, Milne Bay	3	10				
	Buka Passage, Bougainville I.	2	2				
CORAL SEA:	Bootless Bay, Port Moresby			2	3		
	Pari, Port Moresby			1	2		
	Port Moresby, main wharf	19	47				
	Port Moresby Harbour			1	1		
	Coglan Head, Port Moresby Harbour	1	11	4	6		
	Napa Napa, Port Moresby Harbour	3	3				
	Fairfax Harbour, Port Moresby			2	2		
	Roku Bay, Port Moresby			1	3		
	Idler's Bay, Port Moresby			2	3		
<i>Teredo fulleri</i> (Clapp) 1924 (marine)							
BISMARCK SEA:	Namatanai, New Ireland	2	14				
	Tuskul, wharf, New Hanover I.	1	1				
	Vanimo, New Guinea coast	1	1				
SOLOMON SEA:	Buka Passage, Bougainville I.	3	28				
	Esa'ala, Normanby I.	3	27				
	Bwagaioia, Misima I.	1	1				
CORAL SEA:	Napa Napa, Port Moresby Harbour	1	2				
<i>Teredo poculifer</i> (Iredale) 1936 (brackish water)							
CORAL SEA:	Gonema River (3 sites), Marshall Lag.	15	44				
<i>Teredo somersi</i> (Clapp) 1924 (marine)							
BISMARCK SEA:	Lorengau, wharf, Manus I.	1	1				
	Namatanai, New Ireland	1	4				
	Dami, West New Britain	1	1				
	Madang, wharf, New Guinea coast	3	13				
	Madang, beach, New Guinea coast					1	1
SOLOMON SEA:	Alotau, Milne Bay	1	3				
	Esa'ala, wharf, Normanby I.	2	2				
	Buka Passage, Bougainville I.	3	4				
CORAL SEA:	Port Moresby, wharf	2	4				

		Fixed Timber		Mangrove		Driftwood	
		Coll	Spec	Coll	Spec	Coll	Spec
<i>Spathoteredo obtusa</i> (Sivickis) 1928 (marine)							
BISMARCK SEA:	Lorengau, Manus I., Admiralty Is			1	7		
	Langendrowa Village, Rambuyto I.					1	8
	Sopa Sopa Head, Manus I.			1	7		
	Rambuyto I., Admiralty Is					1	216
	Tuskul, wharf, New Hanover	2	24				
	Dami, West New Britain	2	2				
	Madang, wharf, New Guinea coast	3	17				
	Wewak, beach, New Guinea coast			1	2		
	Wewak, wharf, New Guinea coast	1	5				
SOLOMON SEA:	Alotau, Milne Bay	1	1				
	Bwagaoia, wharf, Misima I.	2	2				
	Loaga Creek, Bwagaoia, Misima I.	1	5				
	Esa'ala, wharf, Normanby I.	1	1				
	Buka Passage, Bougainville I.	2	8				
	Kieta, Bougainville I.			1	5		
	Pok Pok I., beach, Kieta			1	19		
	Pok Pok I., Estuary, Kieta			1	8		
	Sideia I., Milne Bay					1	2
	Kwato I., China Straits, Milne Bay			1	8		
	Loani, China Straits, Milne Bay					1	2
<i>Nototeredo edax</i> (Hedley) 1895 (euryhaline marine)							
BISMARCK SEA:	Lorengau, estuary, Manus I.			1	1		
	Rabaul, New Britain	5	8				
	Warangoi River, NE New Britain					1	1
	Madang, wharf, New Guinea coast	7	22				
	Vanimo, New Guinea coast	1	2				
SOLOMON SEA:	Lae, wharf, Huon Gulf	1	1				
	Lake Labu, Lae, Huon Gulf			2	13		
	Beama River, mouth, Oro Bay	1	88				
	Alotau, Milne Bay	2	4				
	Kangu Beach, Buin, Bougainville I.	1	1				
	Sideia I., Milne Bay					1	2
CORAL SEA:	Kupiano Wharf, Marshall Lag.	1	1				
	SW McFarlane Harbour, Marshall Lag.			1	1		
	Gonema River (2 sites), Marshall Lag.			2	2		
	Bootless Bay, Port Moresby			1	1		
	Port Moresby, wharf	1	1				
	Coglan Head, Port Moresby Harbour			4	9		
	Napa Napa, Port Moresby Harbour	2	5				
	Hourata Bay, Port Moresby Harbour			1	5		
	Roku Bay, Port Moresby			3	4		
	Kerema Bay, wharf	1	2				
<i>Nausitora dunlopei</i> (Wright) 1864 (brackish water)							
BISMARCK SEA:	Lorengau, river, Manus I.			2	23		
	Escape Bay, Simpson's Harbour, Rabaul			1	10		
	Vulcan Point Lagoon, Rabaul			1	9		
	Wewak, estuary, New Guinea coast			1	2		

		Fixed Timber		Mangrove		Driftwood	
		Coll	Spec	Coll	Spec	Coll	Spec
SOLOMON SEA:	Lae, wharf, Huon Gulf	3	16				
	Labu Lake, Huon Gulf			1	2		
	Beama River, Oro Bay	1	30				
	Cape Killerton, Morobe coast					1	52
	Bubuleta, NE Milne Bay			1	2		
	Gumini River, Alotau, Milne Bay	1	2				
	Sewa Bay, Normanby I.					1	12
	Loaga Creek, Bwagaoia, Misima I.	1	1				
	Pok Pok I., river, Bougainville I.			1	8		
	Ieta River, Buka, Bougainville I.			1	1		
	Kangu Beach, Buin, Bougainville I.	1	11				
	Sideia I., Milne Bay					1	2
	Loani, Milne Bay					1	1
CORAL SEA:	Kupiano Wharf, McFarlane Harbour	2	2				
	SW McFarlane Harbour, Marshall Lag.	6	11	2	2		
	Wanigela Village, Marshall Lag.	2	3				
	Gonema River (8 sites), Marshall Lag.	80	2453	24	232		
	Idler's Bay, Port Moresby			2	2		
	Petoi, Kerema Bay			1	13		
	Kerema Bay, wharf	9	93				
	Mariapepia, Pie River, Gulf			1	1		
	Pie River, Gulf			4	13		
	Kikori, Kikori River	2	86				
	Oriomo River, West Papua	1	4	1	25		

Nausitora n.sp.
(undescribed, marine)

BISMARCK SEA:	Wewak, wharf, New Guinea coast	1	2				
	Wewak, beach, New Guinea coast					1	2
SOLOMON SEA:	Lae, Sugarloaf, Huon Gulf			1	32		

Nausitora hedleyi (Schepman) 1919
(brackish water)

BISMARCK SEA:	Rabaul, New Britain	1	1				
	Wewak, Wom Point, New Guinea coast			1	1		
SOLOMON SEA:	Lae, wharf, Huon Gulf	5	358				
	Lake Labu, Lae, Huon Gulf			2	22		
	Pok Pok River, Kieta, Bougainville I.			1	2		
CORAL SEA:	SW McFarlane Harbour, Marshall Lag.	2	2	1	46		
	Kupiano Wharf, McFarlane Harbour	3	4				
	Wanigela Village, Marshall Lag.	3	4				
	Gonema River (6 sites), Marshall Lag.	62	697	11	34		
	Port Moresby, main wharf	1	1				
	Laloki River, mouth, Galley Reach			1	4		
	Galley Reach, upstream			1	2		
	Murua River, Kerema	1	82				
	Kerema Bay, wharf			1	4		
	Pie River, Baimuru, West Papua			2	12		
	Oriomo River, West Papua	1	2	4	89		

Nausitora globosa (Sivickis) 1928
(brackish water)

BISMARCK SEA:	Tuskul, New Hanover	1	2				
	Warangoi River, NE New Britain			1	15		
	Dami, West New Britain	1	1				
	Madang, wharf, New Guinea coast	2	2				

		Fixed Timber		Mangrove		Driftwood	
		Coll	Spec	Coll	Spec	Coll	Spec
SOLOMON SEA:	Lae, wharf, Huon Gulf	3	139				
	Lake Labu, Huon Gulf			1	2		
CORAL SEA:	Kupiano Wharf, McFarlane Harbour	13	74				
	SW McFarlane Harbour, Marshall Lag.	12	226	1	15		
	Wanigela Village, Marshall Lag.	3	17				
	Gonema River (5 sites), Marshall Lag.	24	146	1	2		
	Port Moresby, wharf	1	1				
<i>Bankia carinata</i> (Gray) 1827 (marine)							
BISMARCK SEA:	Ponam I., Admiralty Is					1	59
	Langendrowa Passage, Rambuyto I.					1	1
	Rabaul, New Britain	1	3				
	Madang, wharf, New Guinea coast	1	1				
	Madang, beach, New Guinea coast					1	2
	Vanimo, New Guinea coast	1	2				
SOLOMON SEA:	Lae, wharf, Huon Gulf	1	1				
	Alotau, Milne Bay	1	1				
	Esa'ala, Normanby I.	2	6				
	Buka Passage, Bougainville I.	1	2				
CORAL SEA:	Kupiano Wharf, McFarlane Harbour	4	10				
	SW McFarlane Harbour, Marshall Lag.	1	3	1	1		
	Bootless Bay, Port Moresby			1	1		
	Port Moresby Harbour	1	25			1	9
	Port Moresby, Main Wharf	16	36				
	Napa Napa, Port Moresby Harbour	3	31				
	Lealea, Port Moresby			1	1		
	Kerema Bay, Gulf	1	1				
	Daru I., wharf, West Papua	3	12				
<i>Bankia campanellata</i> (Moll & Roch) 1931 (marine)							
CORAL SEA:	Kerema Bay, Gulf	2	5				
	Daru I., wharf, West Papua	4	73				
<i>Bankia barthelowi</i> (Bartsch) 1927 (marine)							
BISMARCK SEA:	Lorengau, Admiralty Is	2	3				
	Namatanai, New Ireland	1	11				
	Rabaul, New Britain	10	149			1	3
	Pila Pila Beach, Rabaul					1	1
	Ragaga Bay, New Britain	1	1				
	Dami, West New Britain	1	1				
	Madang, wharf, New Guinea coast	4	10				
	Wewak, beach, New Guinea coast					1	2
	Vanimo, wharf, New Guinea coast	2	8				
SOLOMON SEA:	Lae, wharf, Huon Gulf	5	16				
	Oro Bay, Morobe coast	2	3				
	Alotau, Milne Bay	3	6			1	1
	Sideia I., Milne Bay					1	1

		Fixed Timber		Mangrove		Driftwood	
		Coll	Spec	Coll	Spec	Coll	Spec
<i>Bankia bipalmulata</i> (Lamarck) 1801 (marine)							
BISMARCK SEA:	Lorengau, Manus I.	4	21				
	Namatanai, New Ireland	2	33				
	Tuskul, New Hanover	1	1				
	Rabaul, New Britain	9	286				
	Pila Pila Beach, Rabaul					1	2
	Vulcan Point Lagoon, Rabaul			1	2		
	Kokopo, Blanche Bay, New Britain					1	2
	Warangoi River, NE New Britain					1	1
	Ragaga Bay, New Britain	3	127				
	Dami, West New Britain	3	60				
	Madang, beach, New Guinea coast					1	35
	Madang, wharf, New Guinea coast	12	169				
	Wewak, beach, New Guinea coast					1	1
	Vanimo, wharf, New Guinea coast	8	244				
SOLOMON SEA:	Lae, wharf, Huon Gulf	14	403				
	Oro Bay, Morobe coast	3	83				
	Alotau, Milne Bay	5	16				
	Esa'ala, Normanby I.	3	15				
	Bwagaioia, Misima I.	2	49				
	Buka Passage, Bougainville I.	3	3				
	Kangu Beach, Buin, Bougainville I.	1	4				
CORAL SEA:	Kupiano Wharf, McFarlane Harbour	2	3				
<i>Bankia johnsoni</i> (Bartsch) 1927 (marine)							
BISMARCK SEA:	Lorengau, Manus I., Admiralty Is	3	3				
	Rambuyto I., Admiralty Is					1	1
	Tuskul, New Hanover	1	1				
	Rabaul, New Britain	9	309				
	Dami, West New Britain	3	42				
	Ragaga Bay, West New Britain	2	34				
	Madang, wharf, New Guinea coast	4	15				
	Vanimo, New Guinea coast	5	12				
SOLOMON SEA:	Lae, wharf, Huon Gulf	1	6				
	Oro Bay, Morobe coast	1	1				
	Sewa Bay, Normanby I.					1	23
	Esa'ala, Normanby I.	1	1				
	Alotau, Milne Bay	2	29				
	Kangu Beach, Buin, Bougainville I.	1	2				
	Loani, Milne Bay			1	1		
CORAL SEA:	Kupiano Wharf, Marshall Lag.	5	5				
	Port Moresby, wharf	1	1				
<i>Bankia australis</i> (Calman) 1920 (marine)							
BISMARCK SEA:	Rabaul, New Britain	2	20				
	Madang, wharf, New Guinea coast	2	2				
	Vanimo, wharf, New Guinea coast	1	2				
SOLOMON SEA:	Cape Killerton, Morobe coast					1	3
	Sideia I., Milne Bay					1	16
	Pok Pok I., river, Bougainville I.			1	1		

		Fixed Timber		Mangrove		Driftwood	
		Coll	Spec	Coll	Spec	Coll	Spec
<i>Bankia gracilis</i> (Moll) 1935 (marine and brackish water)							
BISMARCK SEA:	Lorengau, estuary, Manus I.			1	1		
	Rabaul, New Britain	1	1				
	Madang, beach, New Guinea coast					1	1
	Wewak, beach, New Guinea coast					1	1
	Wewak, estuary, New Guinea coast			1	14		
	Vanimo, wharf, New Guinea coast	1	1				
SOLOMON SEA:	Lae, wharf, Huon Gulf	3	5				
	Lake Labu, Lae, Huon Gulf			1	1		
	Beama River, Oro Bay, Morobe coast	1	4				
	Sewa Bay, Normanby I.			1	1		
	Kangu Beach, Buin, Bougainville I.	1	1				
	Cape Killerton, Morobe coast					1	2
CORAL SEA:	Kupiano Wharf, Marshall Lag.	21	311				
	SW McFarlane Harbour, Marshall Lag.	20	97	4	21		
	Wanigela Village, Marshall Lag.	9	72				
	Gonema River (2 sites), Marshall Lag.	6	18				
	Bootless Bay, Port Moresby			3	28		
	Port Moresby, wharf	4	5				
	Coglan Head, Port Moresby Harbour			7	16		
	Hourata Bay, Port Moresby Harbour			1	2		
	Hanuabada Village, Port Moresby	1	1				
	Kanudi, Port Moresby-Harbour			2	6		
	Fairfax Harbour, Port Moresby			2	6		
	Roku Bay, Port Moresby			1	4		
	Idler's Bay, Port Moresby			3	27		
	Galley Reach, upstream			1	30		
	Kerema Bay, wharf	10	124				
	Petoi, Kerema Bay			1	7		
	Daru I., West Papua	2	3				
<i>Bankia rochi</i> (Moll) 1931 (marine and brackish water)							
BISMARCK SEA:	Rabaul, New Britain	1	2				
	Warangoi River, NE New Britain					1	2
CORAL SEA:	Kupiano Wharf, McFarlane Harbour	1	1				
	SW McFarlane Harbour, Marshall Lag.	8	31	2	8		
	Gonema River (1 site), Marshall Lag.	2	4				
	Motupore I., Bootless Bay			1	1		
	Coglan Head, Port Moresby Harbour			1	1		
	Laloki River, mouth, Galley Reach			1	22		
	Galley Reach, upstream			1	1		
	Kerema Bay, wharf			1	4		
	Pie River, Gulf			4	26		
	Daru I., West Papua	3	17				
	Oriomo River, mouth, West Papua	1	12	1	3		
<i>Bankia bipennata</i> (Turton) 1819 (marine)							
BISMARCK SEA:	Ponam I., Admiralty Is					1	3
	Rabaul, New Britain	2	3				

		Fixed Timber		Mangrove		Driftwood	
		Coll	Spec	Coll	Spec	Coll	Spec
<i>Bankia philippinensis</i> (Bartsch) 1927 (marine)							
BISMARCK SEA:	Rabaul, New Britain	5	14				
	Warangoi River, NE New Britain					1	1
	Reiven, NE New Britain					1	1
	Kokopo, Blanche Bay, New Britain					1	1
	Ragaga Bay, New Britain	3	23				
	Dami, West New Britain	3	9				
	Madang, wharf, New Guinea coast	4	11				
	Vanimo, New Guinea coast	2	8				
SOLOMON SEA:	Oro Bay, Morobe coast	3	4				
	Alotau, Milne Bay	4	34				
CORAL SEA:	Kerema Bay, wharf	3	10				
	Daru I., West Papua	3	7				
	Oriomo River, mouth, West Papua	1	14				
<i>Bankia nordi</i> (Moll) 1935 (marine)							
BISMARCK SEA:	Rabaul, New Britain	1	1				
SOLOMON SEA:	Lae, Huon Gulf	2	2				

The Ceratioid Anglerfishes of Australia

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ABSTRACT. Ceratioid anglerfishes recently collected from Australian waters and primarily housed at the Australian Museum, Sydney, represent eight of the 11 recognized families of the suborder, including 12 genera and 15 species, one of which is here described as new. These are listed below together with all additional records of ceratioids from Australian waters. Revised and supplemental diagnostic and descriptive data as well as notes on geographic distribution are included. Pending the chance of subsequent discovery of any as yet unrecorded ceratioids from Australian waters, diagnoses of all families of the Ceratioidei and references to all recent family revisions are provided.

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Mid-water trawling off eastern Australia in the last ten years has amassed a collection of ceratioid anglerfishes housed at the Australian Museum in Sydney that represents eight of the 11 recognized families of the suborder, 12 genera and 15 species, one of which is here described as new. These are listed below together with all additional records of ceratioids from Australian waters. Keys, revised and supplemental diagnostic and descriptive data as well as notes on geographic distribution are also provided. Since most of the approximately 130 recognized species of the Ceratioidei appear to be very widely distributed, diagnoses and key to all families of the Ceratioidei are provided on the plausible chance that representatives will turn up in Australian waters.

Methods and Materials

Australian waters are defined as that area lying within 200 miles of the Australian continent.

Standard lengths (SL) are used throughout. Terms are defined as follows: *illicium*: the first dorsal spine that bears a terminal bait; *esca*: the fleshy bait at the tip of the first dorsal spine; *denticular*: small, tooth-bearing ossification present in the skin of the snout above the symphysis of the premaxillae and at the tip of the lower jaw of male ceratioids (Bertelsen, 1951); *caruncle*: fleshy, club-shaped light-organ situated on the dorsal mid-line just anterior to the soft dorsal fin of females of the Ceratiidae. Methods for taking counts and measurements, and terminology used in describing esca morphology, follow Pietsch (1974, fig. 60).

Only material in the collections of the Australian Museum, Sydney (AMS) and the Western Australian Museum, Perth (WAM), is listed. All specimens were collected by the Fisheries Research Vessel "Kapala" with an Engel Midwater Trawl, unless otherwise indicated. Material from other sources referred to in the descriptions is catalogued in the following institutions:

BMNH: British Museum (Natural History), London

IOAN: Institution of Oceanology, Academy of Sciences of the USSR, Moscow

ISH: Institut für Seefischerei, Hamburg

LACM: Natural History Museum of Los Angeles County

USNM: National Museum of Natural History, Washington DC

ZMB: Zoologisches Museum der Humboldt-Universität zu Berlin

ZMUC: Zoological Museum, University of Copenhagen

All material is female unless otherwise indicated.

Suborder CERATIOIDEI

Diagnosis. Most distinctly differing from other suborders of Lophiiformes in being bathy- and mesopelagic, lacking pelvic fins (except in larval and newly metamorphosed *Caulophryne*) and having extreme sexual dimorphism. Most females have a single external cephalic fin-ray, illicium with esca photophore (illicium absent in *Neoceratias* and esca bulb and photophore lacking in *Caulophrynidae* and *Rhynchactis*; an external second cephalic ray present in juvenile *Diceratiidae* and *Ceratiidae*). Males are

dwarfed, much smaller than the adult females; they lack esca and external illicium, have enlarged eyes and/or olfactory organs, and have pincer-like jaws with hooked denticular teeth, assumed to be used for attachment to

the females; in some families and genera this attachment becomes parasitic through fusion of male and female tissue.

Key to the Families of the Ceratioidei

1. Illicium absent 2
- Illicium present; females 3
2. Long hooked teeth on outer sides of jaws females of Neoceratiidae, p.93
- No teeth on outer sides of jaws (males of all families) 14
3. No bulbous light organ on tip of illicium 4
- A bulbous light organ on tip of illicium 5
4. Longest rays of dorsal and anal fin greater than 60% of SL;
body short Caulophrynidae, p.79
- Longest rays of dorsal and anal fin much less than 60% SL; body
elongate *Rhynchactis* of Gigantactinidae
5. More than 11 dorsal rays Melanocetidae, p.80
- Fewer than 11 dorsal rays 6
6. Two or three caruncles on dorsal midline; cleft of mouth vertical to
strongly oblique Ceratiidae, p.89
- No caruncles on dorsal midline; cleft of mouth nearly horizontal 7
7. A second cephalic ray present immediately posterior to base of illicium,
bearing a distal luminous gland (withdrawn beneath skin in larger
specimens, its presence indicated by small pore) Diceratiidae, p.83
- A second cephalic ray absent 8
8. Upper jaw extending anteriorly far beyond lower jaw; esca with 1–3
denticles Thaumatoichthyidae, p.89
- Jaws equal anteriorly; esca without denticles 9
9. Illicium emerging on tip of snout, length of head less than 35% of SL,
length of caudal peduncle more than 20% of SL;
5 pectoral radials *Gigantactis* of Gigantactinidae, p.91
- Illicium emerging behind tip of snout; length of head more than 35%
of SL; caudal peduncle less than 20% of SL; 3–4 pectoral radials 10
10. Dermal spines or plates present 11
- Skin naked (although microscopic spinules may be present, skin appears
naked and smooth) 12
11. Skin with some large, bony plates, each bearing a median
spine specimens larger than 30–40 mm of Himantolophidae, p.82
- Skin with numerous, close-set spines Centrophrynidae, p.89
12. Four to five branchiostegal rays; D.3 (very rarely 2 or 4); A.3 (rarely
2 or 4) Linophrynidae, p.94
- Six branchiostegal rays; D. more than 4; A. 4–7 13

13. Snout and chin more or less pointed Oneirodidae, p.83
- Snout and chin very blunt specimens of less than 30–40 mm of Himantolophidae, p.82
14. Upper denticular teeth absent; A. more than 9 15
- Upper denticular teeth present; A. less than 9 16
15. Lower denticular with approximately 9 teeth; young specimens with ventral fins; D. 14–22; A. 13–19 Caulophrynidae¹, p.79
- Lower denticular trifurcated, each branch with a double hook; D.11–13; A.10–13 Neoceratiidae, p.93
16. Olfactory organs small; eyes large, bowl-shaped; D.3–5; A.3–5 Ceratiidae, p.89
- Olfactory organs large; eyes not bowl-shaped 17
17. More than 11 dorsal rays Melanocetidae, p.80
- Fewer than 11 dorsal rays 18
18. Fewer than 5 dorsal rays 19
- 5–8 dorsal rays 20
19. Eyes large, slightly tubular, directed more or less anteriorly; D.3, rarely 2 or 4; A.3, rarely 2 or 4 Linophrynidae, p.94
- Eyes spherical, directed laterally; D.4; A.4, rarely 3 *Rhynchactis* of Gigantactinidae
20. Eyes small, diameter 5% of SL or less 21
- Eyes large, diameter greater than 5% SL 22
21. A small digitiform hyoid barbel, 6 branchiostegal rays Centrophrynidae, p.89
- No hyoid barbel; 5 branchiostegal rays Gigantactinidae, p.89
22. Skin completely covered with well developed spines; anterior nostrils opening laterally 23
- Skin spines absent or small and scattered; anterior nostrils opening forward near end of snout 24
23. Several (more than 10) upper denticular teeth, all fused at base Himantolophidae, p.82
- Two separate upper denticular teeth Diceratiidae, p.83
24. Small, but distinct spines scattered in skin of body Thaumichthyidae², p.89
- Skin spines absent or microscopic in size Oneirodidae³, p.83

Notes: ¹Males of the caulophrynid genus *Robia*, which has D.6, A.5, are unknown.

²Males of the thaumichthyid genus *Lasiognathus*, in which the females have naked skin, are unknown.

³Males of 8 of the 15 recognized oneirodid genera are unknown, including *Spiniphyrne* in which the females have spiny skin.

Family CAULOPHRYNIDAE

Diagnosis. Females are distinguished from those of other ceratioid families by having extremely elongate dorsal and anal rays; eight caudal rays; neuromasts of the acoustico-lateralis system located at the tips of

extremely elongate filaments; two pectoral radials; escal bulb absent.

Males become parasitic; free-living stages are distinguished from those of other ceratioid families by the absence of an upper denticular; lower denticular unbranched bearing approximately nine teeth; ventral

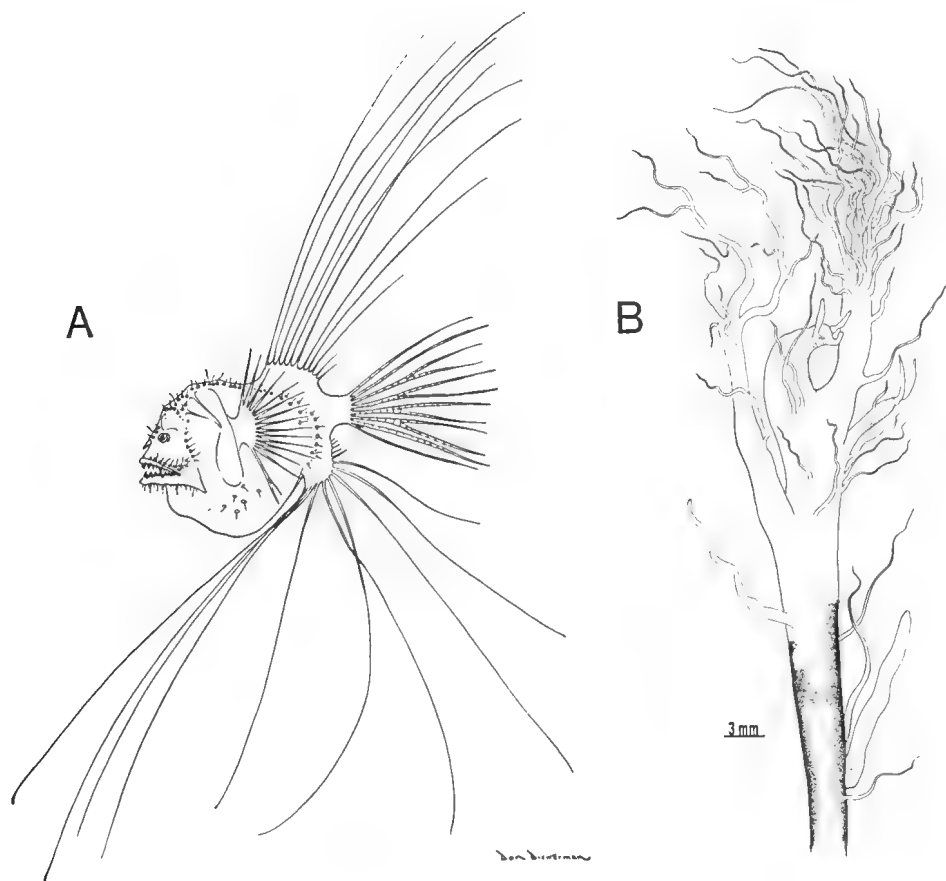


Fig. 1. *Caulophryne jordani* Goode and Bean, 1896. A, after Beebe and Rose (1926). B, esca in left lateral view, LACM 33924-1, 54 mm SL; after Pietsch (1979).

fins present in younger stages.

Two genera, one recorded from eastern Australian waters.

Caulophryne Goode and Bean, 1896

For synonymy see Pietsch, 1979.

Diagnosis. Males and females are distinguished from those of *Robia* (the only other genus of the family) in having D. 14–22 and A. 12–19. Females are further distinguished in having a considerably shorter illicium (less than 50% SL).

Three species, one recorded from eastern Australian waters.

Caulophryne jordani Goode and Bean, 1896 Fig. 1

Caulophryne jordani Goode and Bean, 1896:26, 496, 541, fig. 409 (original description, single specimen off Long Island, New York, holotype USNM 39265).—Pietsch, 1979:12, 15–16, figs 1–13, 16, 18, 19, 24 (family review based on all known material).

For complete synonymy see Pietsch, 1979.

Material. A single female: AMS 1.20314-017, 64.5 mm SL, east of Broken Bay, N.S.W., 33° 28' S, 152° 33' E, 0–900 m over 2400 m, 14 December 1977.

Caulophryne jordani was previously known from eleven specimens collected from widely separated stations in all three major oceans (Pietsch, 1979, fig. 24). Although represented by a single specimen from the Pacific Sector of the Southern Ocean (at approximately 39° 58' S, 160° 34' E, the individual recorded here is the first record of a metamorphosed caulophrynid from Australian waters. However, a single larval specimen (ZMUC P92202) tentatively referred to *C. jordani* was recorded from this area (33° 33' S, 154° 04' E) by Bertelsen (1951:34).

Two additional caulophrynids are known from the Indo-Australian Archipelago: *Robia legula*, represented only by the holotype (LACM 36024-1) collected in the Banda Sea, and *Caulophryne pelagica*, a single specimen (LACM 36023-1) from the Halmahera Sea.

Family MELANOCETIDAE

Diagnosis. Males and females are distinguished from those of other ceratioid families by having D. 12–17 and A.4 (rarely 3 or 5). Females are further distinguished by the absence of sphenotic spines and skin spines (although spines are present microscopically, the skin appears naked and smooth).

Males are non-parasitic with skin spinulose or naked; upper denticular teeth with 2–3 semicircular series of strong, recurved denticles, fused with a median series of 3–9 enlarged dermal spines that articulate with the pterygiophore of the illicium; lower denticular with 10–23 recurved denticles, fused into a median and two lateral groups; eyes and nostrils lateral; nasal area unpigmented, inflated.

A single genus.

Melanocetus Günther, 1864

For synonymy see Pietsch and Van Duzer, 1980.

With the characters of the family.

Five species, two recorded from Australian waters.

Key to Females of Species of *Melanocetus* Recorded from Australian Waters

1. Anterior margin of vomer nearly straight; esca bulb with compressed posterior and (usually) anterior crests; width of esca bulb 3.8–8.6% of SL *Melanocetus johnsoni* Günther, 1864
- Anterior margin of vomer deeply concave; esca bulb without posterior and anterior crests; width of esca bulb 1.9–5.1% of SL *Melanocetus murrayi* Günther, 1887

Key to Males of Species of *Melanocetus* Recorded from Australian Waters

1. A median series of 11 or more denticular teeth on snout; 12–24 denticular teeth on lower jaw; D. 13–15; P. 17–21 *Melanocetus johnsoni* Günther, 1864
- A median series of 3–5 denticular teeth on snout; 10–13 denticular teeth on lower jaw; D. 12–14; P. 15–18 *Melanocetus murrayi* Günther, 1887

Melanocetus johnsoni Günther, 1864

Fig. 2

Melanocetus johnsoni Günther, 1864: 301–303, pl. 25 (original description, single specimen from Madeira, holotype BMNH 1864.7.18.6.—Pietsch and Van Duzer, 1980:59–87 (family review based on all known material).

For complete synonymy see Pietsch and Van Duzer, 1980.

Material. Sixty-six females, 4–88 mm SL: AMS 1.16162–019, 6 (12–26 mm SL), E of Sydney, N.S.W., 34°05'S, 151°55'E, 0–950 m over 1920–2830 m, 25 March 1971. AMS I.19562–041, 4 (4–9 mm SL), E of Port Hacking, N.S.W., 34°09'S, 152°07'E, 0–550 m over 1890 m, 23 March 1971. AMS I.19601–036, 25 (5–11 mm SL), E of Sydney, N.S.W., 34°10'S, 151°59'E, 0–75 m over 1810–2470 m, 24 March 1971. AMS I.19608–026, 4 (4–8 mm SL), off Sydney, N.S.W., 34°05'S, 151°56'E, 0–800 m over 2410–2920 m, 23 March 1971. AMS I.20064–029, 21.5 mm SL, off Sydney, N.S.W., 34°10'S, 152°04'E, 0–660 m over 2500 m, 26 October 1977. AMS I.20066–002, 5 (11–22.5 mm SL), E of

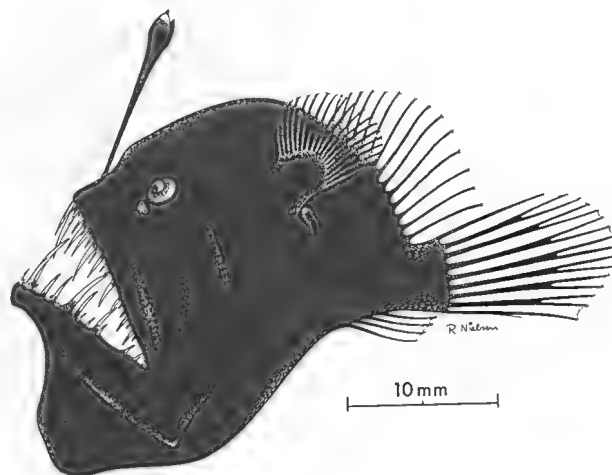


Fig. 2. *Melanocetus johnsoni* Günther, 1864, 25 mm SL, ZMUC P92373. Drawn by R. Nielsen.

Brush Island, N.S.W., 35°36'S, 150°55'E, 0–650 m over 2000 m, 27 October 1977. AMS I.20070–008, 32 mm SL, NE of Cape Howe, N.S.W., 37°24'S, 150°30'E, 0–540 m over 3600 m, 1 November 1977. AMS I.20306–006, 38 mm SL, E of Broken Bay, N.S.W., 33°31'S, 152°20'E, 0–900 m over 1800–2900 m, 12 December 1977. AMS I.20307–012, 2 (17–29 mm SL), E of Broken Bay, N.S.W., 33°28'S, 152°25'E, 0–900 m over 1830–2800 m, 13 December 1977. AMS I.20313–004, 2 (17–26.5 mm SL), E of Tuggerah Lakes, N.S.W., 33°20'S, 152°32'E, 0–450 m over 2400 m, 14 December 1977. AMS I.20314–012, 13 (14–52 mm SL), E of Broken Bay, N.S.W., 33°28'S, 152°33'E, 0–900 m over 4200 m, 14 December 1977. AMS I.20315–008, 12.5 mm SL, E of Sydney, N.S.W., 33°53'S, 152°02'E, 0–900 m over 1800 m, 14 December 1977. AMS I.20410–006, 88 mm SL, E of Wollongong, N.S.W., 34°27'S, 151°38'E, 0–600 m over 2000–2200 m, 23 May 1978.

Sixty-six specimens of *Melanocetus johnsoni* have been collected over the past ten years off the east coast of Australia. The only previous record from this area was a single larval specimen (ZMUC P92307) listed by Bertelsen (1951:263). This species has a wide geographic distribution in tropical and subtropical waters of all three major oceans of the world (Pietsch and Van Duzer, 1980).

Melanocetus murrayi Günther, 1887

Fig. 3

Melanocetus murrayi Günther, 1887:57, pl. 11, fig. A (original description, single specimen from central Atlantic, lectotype BMNH 1887.12.7.17).—Pietsch and Van Duzer, 1980: 59–87 (family review based on all known material). For complete synonymy see Pietsch and Van Duzer, 1980.

Although several records are known from Indonesian waters (Pietsch and Van Duzer, 1980, fig. 30), *Melanocetus murrayi* is represented in Australian waters by a single metamorphosed female (BMNH 1932.5.3.1) collected at approximately 33°33'S, 154°04'E (Regan and Trewavas, 1932:50), and a larval specimen (ZMUC P92438) recorded by Bertelsen (1951:263).

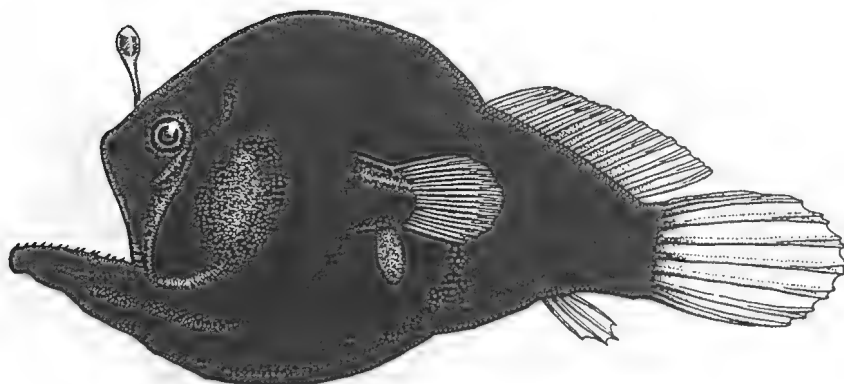


Fig. 3. *Melanocetus murrayi* Günther, 1887, 15 mm SL, BOC 2032. After Parr (1927).

Family HIMANTOLOPHIDAE

Diagnosis. Females are distinguished from those of other ceratioid families by having large, bony plates embedded in the skin, each bearing a median spine; snout and anterior surface of lower jaw with low, rounded, dermal papillae (spines and papillae absent in juveniles less than approximately 30 mm SL); lower jaw very robust, projecting slightly beyond upper; esca bulb large bearing stout, tentacular appendages.

Males are non-parasitic with skin spinulose; upper and lower denticular teeth in 2–3 transverse series fused at the base; eyes and nostrils lateral; nasal area pigmented, not inflated.

A single genus.

Himantolophus Reinhardt, 1837

A complete family review is in preparation by Bertelsen and Krefft.

With the characters of the family.

Fifteen species recognized, one recorded from Australian waters in addition to several unidentifiable specimens.

Himantolophus appellii (Clarke, 1878)

Fig. 4

Aegoeonichthys appellii Clarke, 1878:145, pl.6 (original description, single specimen from off New Zealand, holotype not preserved).—Waite, 1912:194–197, pl.10 (description of an additional specimen from off New Zealand).

Himantolophus appellii.—Regan, 1926: 41–42 (*Aegoeonichthys*, a synonym of *Himantolophus* Reinhardt); Bertelsen, 1952: 60, 66 (family review based on all known material).

Diagnosis. Females are distinguished from those of other members of the genus in having transparent swellings of the distal part of esca bulb surrounding a pair of darkly pigmented appendages; a second pair of tentacular appendages situated posterior to swellings, approximately twice as long as the first pair, and divided into three or more branches; in specimens greater than

approximately 30 mm SL, two to five shorter, bifurcated or unbranched tentacular appendages behind and below posterior distal pair (Fig. 4A).

Material. 17 females, 20–270 mm SL: AMS I.16162–018, 39 mm SL, E of Sydney, N.S.W., 34°05'S, 151°55'E, 0–950 m over 1920–2830 m, 25 March 1971. AMS I.17868–005, 32 mm SL, E of Sydney, N.S.W., 33°40'S, 151°56'E, otter trawl, 0–425 m, 6 December 1972. AMS I.20071–003, 24 mm SL, E of Kiamà, N.S.W., 34°40'S, 151°15'E, 0–548 m over 3290 m, 3 November 1977. AMS I.20314–013, 38 mm SL, E of Broken Bay, N.S.W., 33°28'S, 152°33'E, 0–900 m over 4200 m, 14 December 1977. AMS I.20410–007, 4, 20–62 mm SL, off Wollongong, N.S.W., 0–600 m over 2000–2200 m, 23 May 1978. AMS I.21365–009, 28 mm SL, off Newcastle, N.S.W., 33°09'S, 153°05'E, 0–750 m over 1500 m, 28 November 1979. AMS I.21411–001, 24.5 mm SL, E of Port Kembla, N.S.W., 34°33'–34'S, 153°42'E, 26 September 1979. AMS I.22648–001, c. 165 mm, off Albany, W.A., 28 November 1974. AMS I.22649–001, off Albany, W.A., 3 April 1974. WAM P 15746, 163 mm SL, off Albany, W.A., June 1964. WAM P 15747, 270 mm SL, 35°16'S, 118°40'E, 1 November 1966. WAM P 15748, 167 mm SL, 35°21'S, 118°30'E, 13 October 1965. WAM P 15749, 190 mm SL, 35°10'S, 118°36'E, 29 August 1964. WAM P 15750, 174 mm, 35°24'S, 118°30'E, 22 September 1964. (All WAM specimens from stomachs of sperm whales.)

Tentatively referred specimens. One female, two males and two larval females: AMS I. 16494–043, 14 mm SL larval female, E of Sydney, N.S.W., 34°02'S, 152°12'E, 0–600 m over 2395–2830 m, 25 March 1971. AMS I.17887–005, 15 mm SL larval female, E of Port Hacking, N.S.W., 34°13'S, 150°22'E, 0–146 m over 165 m, 6 May 1974. AMS I.20305–003, 51 mm SL female, E of Broken Bay, N.S.W., 33°33'S, 152°18'E, 0–170 m over 2000 m, 12 December 1977. AMS I.20307–013, 2 males (23.5–27 mm SL), 70 km E of Broken Bay, N.S.W., 33°28'S, 152°25'E, 0–900 m over 1830–2800 m, 13 December 1977.

Besides the 17 specimens listed above only a single specimen caught off Tasmania (IOAN 40510, 225 mm SL) is known from Australian waters. The holotype and four additional specimens are recorded from off New Zealand and six additional specimens have been caught in the Atlantic and Indian Oceans. All the records are within a narrow zone between 32°S and 43°S from the



Fig. 4. *Himantolophus appellii* (Clarke, 1878) A, esca in left lateral view, 39 mm SL, AMS I.16162-018. B, 38 mm SL, AMS I.20314-013. Drawn by R. Nielsen.

east coast of South America to New Zealand. As no other species of *Himantolophus* has been reported from similar southern latitudes, the eight larvae (3-6 mm total length, ZMUC P92661-92663) previously recorded from this area by Bertelsen (1951:263), as well as the 5 tentatively referred specimens listed above, most probably represent this species. Among the latter the 51 mm SL female has lost the esca, but in all other characters it is quite similar to the material of *H. appellii* described above.

The two metamorphosed males (23.5-27 mm SL) have 15-18 upper and lower denticular teeth in 2-3 irregular series; 10-12 olfactory lamellae; posterior nostril nearly as large as, and well separated from, eye. To what extent *Himantolophus* males may show specific differences in these characters is unknown.

The two larval females (14-15 mm SL) are in good agreement with *Himantolophus* larvae of similar size described by Bertelsen (1951:61-63) and Maul (1962:11-12). The inflated transparent skin has no dorsal pigment spot, but several melanophores are present, scattered below and in front of the gill opening.

Family DICERATIIDAE

Diagnosis. Females are distinguished from those of other ceratioid families by having a second cephalic ray bearing a distal luminous gland, in young specimens appearing as a club-shaped ray immediately behind the illicium, in larger specimens withdrawn beneath skin, its presence indicated by a small pore. They may further be distinguished by the following combination of characters: opercle bifurcate; subopercle with well-developed anterior spine; sphenotic spines present; hyomandibular with double head; three pectoral radials;

microscopic dermal spines present; D.5-7; A.4; P.13-16. Males probably non-parasitic; skin spinulose; two denticular teeth on snout and two transverse series each of 4-5 on lower jaw, all separate; eyes and nostrils lateral (Bertelsen, 1983).

No member of the family Diceratiidae has been recorded from eastern Australia. Two species, however, are known from adjacent Indonesian waters: *Diceratias bispinosus* (Paxton and Lavenberg, 1973) and *Phrynichthys thele*. For a complete family review see Uwate (1979).

Family ONEIRODIDAE

Diagnosis. The numerous and variously specialized genera of the Oneirodidae have few common features that distinguish them from other ceratioid families. Although not characteristic of all genera, the following features are useful in differentiating Australian oneirodids: opercle bifurcate; three pectoral radials; hyomandibular with a double head (single head in *Bertella*); anterior subopercular spine usually absent (blunt projection present in most specimens of *Chaenophryne*, adolescent females of *Lopholodops* and some larvae and males of *Dolophichthys* and *Pentherichthys*); skin spines absent (microscopic dermal spines present in *Oneirodes*); D.4-8, A.4-7, P.14-30.

Males are non-parasitic with skin naked; posterior end of upper denticular remote from anterior end of pterygiophore of illicium; eyes and posterior nostrils lateral, anterior nostrils close together and directed anteriorly; olfactory organs large; nasal area with or without pigment.

Fifteen genera (see Pietsch, 1974, 1978), only three recorded from Australian waters.

**Key to Females of Genera and Species of the
Oneirodidae Recorded from Australian Waters**

1. Sphenotic spines present; opercle deeply notched posteriorly; pelvic bones rod-shaped, not expanded or only slightly expanded distally 2
- Sphenotic spines absent; opercle not deeply notched posteriorly; pelvic bones widely expanded distally, occasionally triradiate *Chaenophryne draco* Beebe, 1932, p.88
2. Caudal fin not covered by black skin except at base; anal fin rays 4, rarely 5; subopercle short and broad, lower part nearly circular (*Oneirodes*) 3
- Caudal fin covered by black skin for some distance beyond fin base; anal fin rays 5, rarely 4; subopercle long and narrow, lower part strongly oval *Dolopichthys pullatus* Regan and Trewavas, 1932, p.87
3. Esca with two or three medial filaments more than six times length of escal bulb (Fig. 5) *Oneirodes krefftii* Pietsch, 1974, p.84
- Esca without elongate medial appendages 4
4. Anterior escal appendage laterally compressed; posterior escal appendage less than half length of escal bulb (Fig. 6) *Oneirodes sabex* Pietsch and Seigel, 1980, p.85
- Anterior escal appendage cylindrical; posterior escal appendage considerably longer than length of escal bulb; lateral escal appendage present (Fig. 7) *Oneirodes whitleyi* n.sp., p.85

***Oneirodes* Lütken, 1871**

For synonymy see Pietsch, 1974.

Diagnosis. Males and females are distinguished from those of other oneirodid genera in having the subopercle short and broad, lower part (and upper part in males) semicircular; A.4, very rarely 5. Females are further distinguished by having sphenotic spines; dorsal margin of frontal bone strongly curved; pigmented skin not extending beyond base of caudal fin.

Males are further distinguished by having skin between the nostrils unpigmented; inner surface of subopercle unpigmented; caudal peduncle without subdermal pigment; 7–13 lower denticular teeth.

Approximately 33 species, three recorded from eastern Australian waters.

***Oneirodes krefftii* Pietsch, 1974**

Fig. 5

Oneirodes krefftii Pietsch, 1974: 57, figs 60B, 75, 76, 107, tables 1, 12 (original description, 3 specimens from eastern South Atlantic and Indian Ocean, holotype, ISH 1536/71).

Material. A single female, 50 mm SL: AMS I.16162–020. Tasman Sea, off Sydney, N.S.W., 34°05'S, 151°55'E, 0–950 m over 1922–2836 m, 25 March 1971.

This specimen represents the first record of *O. krefftii* since the original description (Pietsch, 1974), and extends the known geographic range of the species into



Fig. 5. Esca of *Oneirodes krefftii* Pietsch, 1974, holotype, 50 mm SL, ISH 1536–7. A, anterolateral view. B, posterolateral view, anterior appendage not shown. After Pietsch (1974).

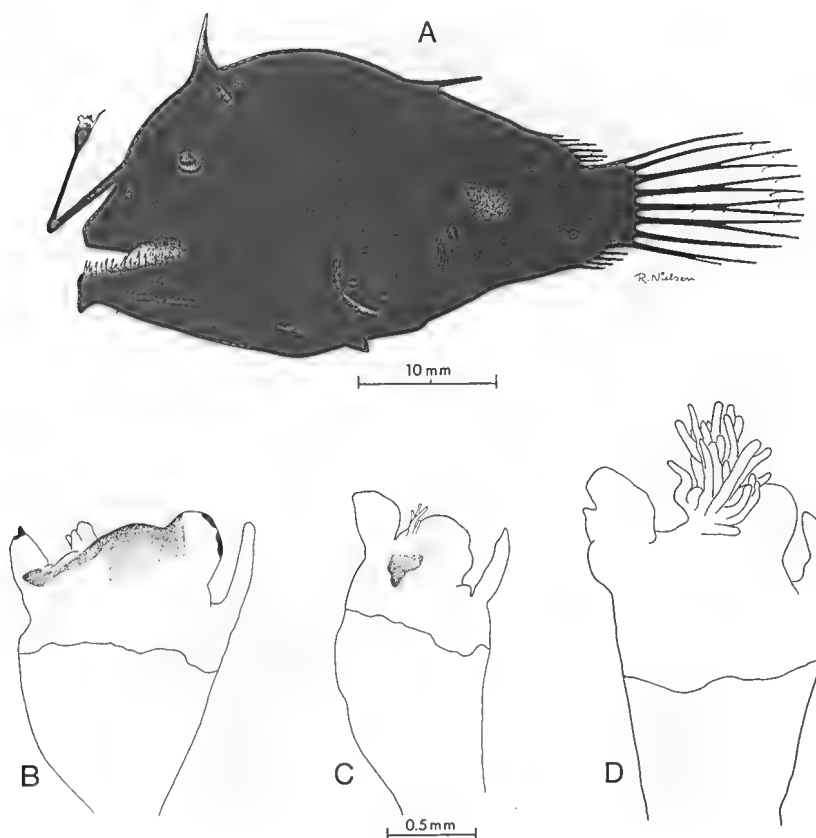


Fig. 6. *Oneiroides sabex* Pietsch and Seigel, 1980. A, paratype, 39 mm SL, AMS I.20314-016. Drawn by R. Nielsen. B-D, escae in left lateral views, after Pietsch and Seigel (1980). B, paratype, 17 mm SL, LACM 36089-4; C, paratype, 26.5 mm SL, LACM 36087-4; D, holotype, 46 mm SL, LACM 36116-3.

the western South Pacific Ocean. Although the esca of this new specimen is somewhat damaged, it compares very well with the type material.

Oneiroides sabex Pietsch and Seigel, 1980

Fig. 6

Oneiroides sabex Pietsch and Seigel, 1980: 387, figs 9, 10 table 3 (original description, 14 specimens from off Luzon, Philippines, Banda Sea and off Sydney, Australia, holotype LACM 36116-3).

Material. Four metamorphosed females (12.5-50 mm SL): AMS I.16162-055, 12.5 mm SL, 72.5 km E of Sydney, N.S.W., 34°05'S, 151°55'E, 0-950 m over 1922-2836 m, 25 March 1971. AMS I.20314-016, paratype, 39 mm SL, E of Broken Bay, N.S.W., 33°28'S, 152°33'E, 0-900 m over 4200 m, 14 December 1977. AMS I.20315-010, paratype, 32.5 mm SL, E of Sydney, N.S.W., 33°53'S, 152°02'E, 0-900 m over 1800 m, 14 December 1977. AMS I.21368-008, 50 mm SL, off Newcastle, N.S.W., 33°04'S, 153°08'E, 0-750 m over +1500 m, 28 November 1979.

The original description of *O. sabex* was based on 14 metamorphosed females collected from south-east Asian and eastern Australian waters (Pietsch and Seigel, 1980). In addition to the two paratypes listed above, two more specimens (12.5-50 mm SL) have been deposited in collections of the Australian Museum.

Oneiroides whitleyi n.sp.

Fig. 7, Table 1

Material. Three metamorphosed females, 11-30 mm SL.

Holotype. AMS I.20066-003, 30 mm SL, east of Brush Island, N.S.W., 35°36'S, 150°55'E, 0-650 m over 2000 m, 27 October 1977.

Paratypes. AMS I.19608-045, 11 mm SL, off Sydney, N.S.W., 34°05'S, 151°56'E, 0-800 m over 2410-2920 m, 23 March 1971. AMS I.20066-070, 22 mm SL, data as for holotype.

Diagnosis. A species of *Oneiroides* differing from all previously described species in the morphology of the esca: anterior appendage cylindrical with a darkly pigmented internal tube and conical distal tip, bearing from 3 to 5 short, lateral filaments; a pair of highly branched medial appendages; posterior appendage cylindrical, unpigmented, approximately one and one-half times length of escal bulb; a cylindrical, lateral appendage on each side, bifurcated distally and bearing 0-1 small, lateral filament (Fig. 7B, C).

Description. Escal appendage pattern B (Pietsch, 1974, fig. 60B); except for tiny differences in numbers and size of filaments quite similar in the three specimens. Subopercle short, upper end rounded, or tapering to a point (in holotype), with slightly concave posterior

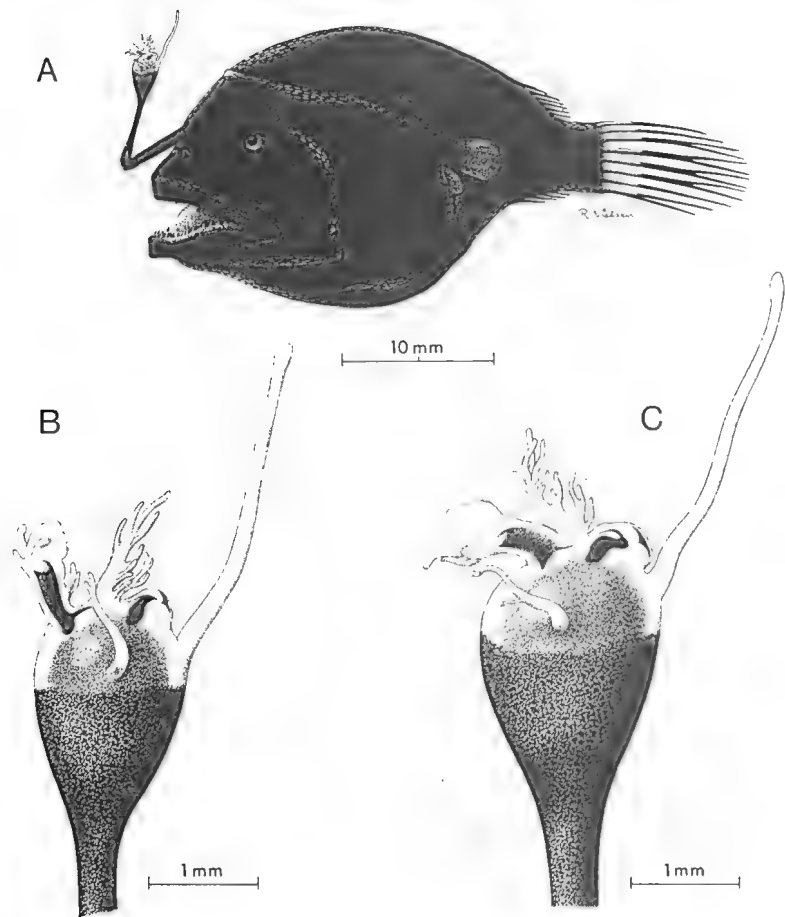


Fig. 7. *Oneirodes whitleyi* new species. A, holotype, 30 mm SL, AMS I.20066-003. B-C, escae in left in lateral views. B, paratype, 22 mm SL, AMS I.20066-070; C, holotype, 30 mm SL, AMS I.20066-003. Drawn by R. Nielsen.

Table 1. Counts and measurements of *Oneirodes whitleyi*. Measurements expressed in per cent of SL.

	Paratype AMS I.19068-045	Paratype AMS I.20066-070	Holotype AMS I.20066-003
Standard Length (mm)	11	22	30
Length			
Head	45	50	47
Lower jaw	50	50	47
Premaxilla	33	30	35
Illicium	27	25	25
Head depth	49	48	48
Teeth			
Vomer	2 + 2	3 + 2	4 + 4
Upper jaw	8 + 8	13 + 12	23 + 21
Lower jaw	12 + 12	18 + 18	20 + 20
Dorsal fin rays	6	6	6
Anal fin rays	4	4	4
Pectoral fin rays	16-16	16-16	16-16

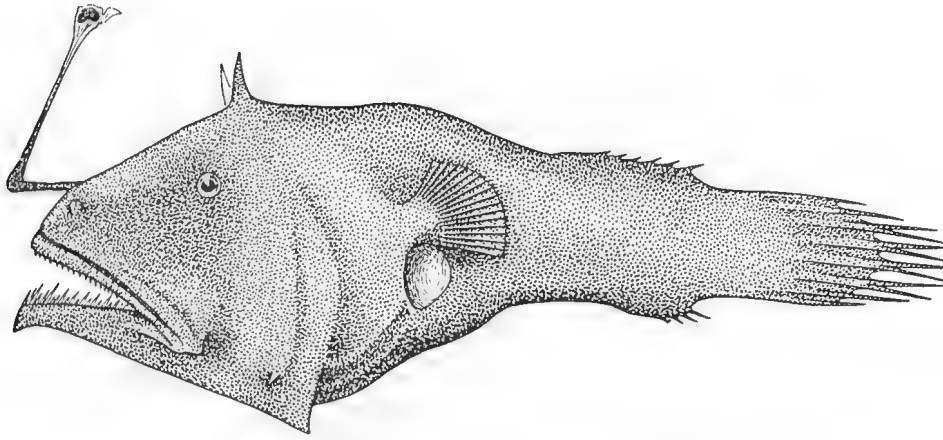


Fig. 8. *Dolopichthys pullatus* Regan and Trewavas, 1932, 32 mm SL, ZMUC P92101. After Regan and Trewavas (1932).

margin; length of lower fork of opercle 30% of SL; ratio of lengths of upper and lower forks of opercle 0.47–0.50. Epibranchial teeth absent; teeth present on pharyngobranchial II.

Counts and measurements in Table 1.

Distribution. *Oneirodes whitleyi* is known only from three metamorphosed females collected from eastern Australian waters, between the surface and approximately 800 m.

Etymology. This new form is named in honour of the late Gilbert P. Whitley in recognition of his contribution to Australian ichthyology.

Oneirodes sp.

Material. AMS I.20070–005, 33.5 mm SL, NE of Cape Howe, N.S.W., 37°24'S, 150°30'E, 0–540 m over 3600 m, 1 November 1977.

Since the esca of this metamorphosed female is badly desiccated, the specimen cannot be identified to species.

Oneirodes sp. larvae

Material. AMS I.19608–019, 4 (7–7.5 mm SL), off Sydney, N.S.W., 34°05'S, 151°56'E, 0–800 m over 2410–2920 m, 23 March 1971.

As is the case with nearly all larvae except those of monotypic ceratioid genera, these four small specimens cannot be identified to species.

Other Species of *Oneirodes*

A considerable number of additional species of *Oneirodes* have been collected from adjacent South-east Asian waters. Any or all of these might be expected to occur off Australia as well (see Pietsch, 1974, and Pietsch and Seigel, 1980):

Oneirodes alius Seigel and Pietsch, 1978

Oneirodes carlsbergi (Regan and Trewavas, 1932)

Oneirodes cristatus (Regan and Trewavas, 1932)
Oneirodes eschrichtii Lütken, 1871
Oneirodes flagellifer (Regan and Trewavas, 1932)
Oneirodes melanocauda Bertelsen, 1951
Oneirodes micronema Grobecker, 1978
Oneirodes plagionema Pietsch and Seigel, 1980
Oneirodes pterurus Pietsch and Seigel, 1980
Oneirodes schistonema Pietsch and Seigel, 1980
Oneirodes schmidtii (Regan and Trewavas, 1932)
Oneirodes thysanema Pietsch and Seigel, 1980

Dolopichthys Garman, 1899

For synonymy see Pietsch, 1972b.

Diagnosis. Males and females are distinguished from those of other oneirodid genera in having the opercle deeply notched posteriorly; subopercle long and narrow, the upper part tapering to a point; A.5, rarely 4. Females are further distinguished by having sphenotic spines; dorsal margin of the frontals bones nearly straight; pigmented skin extending well beyond base of caudal fin.

Males are further distinguished by having nasal area pigmented; posterior nostril contiguous with eye; 4–10 lower denticular teeth.

Six species, only one recorded from eastern Australian waters.

Dolopichthys pullatus Regan and Trewavas, 1932 Fig. 8

Dolopichthys pullatus Regan and Trewavas, 1932:79, fig. 123, pl. 3, fig. 1 (original description, single specimen from the Molucca Sea, holotype ZMUC P92101).—Pietsch, 1972b: 7–12, figs 1–4, 11, 12, tables 1–3 (review based on all known material).

For complete synonymy see Pietsch, 1972b.

Material. Four females, 14–73 mm SL: AMS I.20066–001, 27 mm SL, E of Brush Island, N.S.W., 35°36'S, 150°55'E,

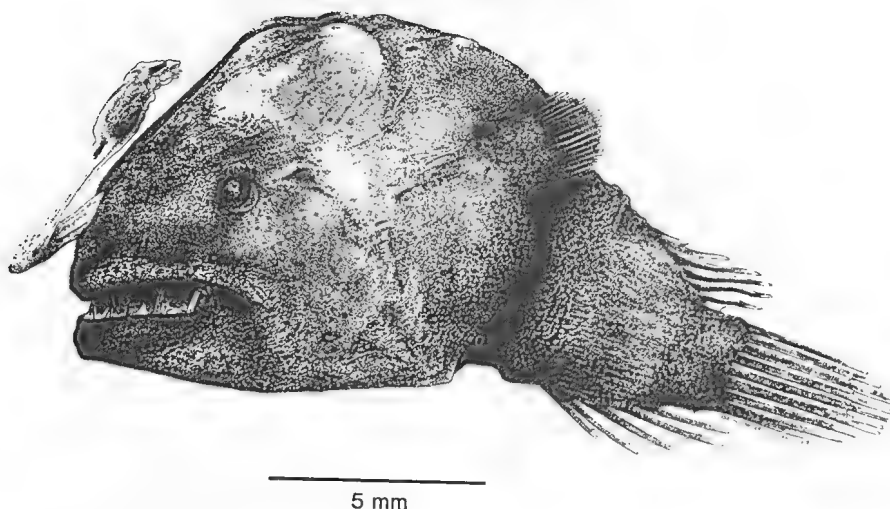


Fig. 9. *Chaenophryne draco* Beebe, 1932. After Munk and Bertelsen (1980).

0–650 m over 2000 m, 27 October 1977. AMS I.20315–011, 26.5 mm SL, E of Sydney, N.S.W., 33°53'S, 152°02'E, 0–900 m over 1800 m, 14 December 1977. AMS I.20410–010, 73 mm SL, E of Wollongong, N.S.W., 34°27'S, 151°38'E, 0–600 m over 2000–2200 m, 23 May 1978. AMS I.21365–010, 14 mm SL, off Newcastle, N.S.W., 33°09'S, 153°05'E, 0–750 m over +1500 m, 28 November 1979.

Four specimens of *Dolopichthys pullatus* are in the collections of the Australian Museum, Sydney. Although more than 30 individuals have been reported from localities in the Atlantic, Gulf of Mexico, eastern Pacific and Indian oceans (Pietsch, 1972b), this species was previously represented in the western Pacific by only the holotype from the Molucca Sea, and by a second specimen (LACM 36116–2) collected in the Banda Sea (Pietsch and Seigel, 1980).

The closely related species *Dolopichthys longicornis* is known from 19 metamorphosed females. Two of these were taken in waters adjacent to Australia: the holotype of *Dolopichthys mucronatus* (ZMUC P92100, = *D. longicornis*) from the South China Sea, and a second specimen from the Banda Sea (Pietsch and Seigel, 1980).

Chaenophryne Regan, 1925b

For synonymy see Pietsch, 1975.

Diagnosis. Males and females are distinguished from other oneirodid genera in having the subopercle long and narrow, the upper end tapering to a point; posterior margin of opercle only slightly concave; A.5, rarely 4. Females are further distinguished by the

absence of sphenotic spines (blunt ridges present on parietals and posttemporals); dorsal margin of frontal strongly curved; pigmented skin extending well beyond base of caudal fin.

Males are further distinguished by having nasal area pigmented; posterior nostril not contiguous with eye; 17–27 lower denticular teeth.

Four species, only one recorded from eastern Australian waters.

Chaenophryne draco Beebe, 1932

Fig. 9.

Chaenophryne draco Beebe, 1932:84, fig. 22 (original description, single specimen from off Bermuda, holotype USNM 170943).—Pietsch, 1975:87–90, figs 1B, 2A, 3–5, 8, 11, 12, tables 1–3, 5 (review based on all known material); Munk and Bertelsen, 1980: 103–129, figs 1–20 (esca morphology). For complete synonymy see Pietsch, 1975.

Material. Two females, 14–52 mm SL: AMS I.20064–005, 52 mm SL, off Sydney, N.S.W., 34°10'S, 152°04'E, 0–660 m over 2500 m, 26 October 1977. AMS I.20314–021, 14 mm SL, E of Broken Bay, N.S.W., 33°28'S, 152°33'E, 0–900 m over 4200 m, 14 December 1977.

Chaenophryne draco has a wide distribution, occurring in all three major oceans (Pietsch, 1975). Although it is known from two metamorphosed females collected in the Banda Sea (Pietsch and Seigel, 1980), the specimens reported here are the first records from Australian waters.

Although relatively common in other parts of the world, the closely related *Chaenophryne longiceps* is represented in the western Pacific by a single

metamorphosed male from the Banda Sea (Pietsch and Seigel, 1980). It is conceivable that this form inhabits eastern Australian waters as well.

Other Oneirodids

A number of additional oneirodids have been collected from adjacent, south-east Asian localities. Any or all of these forms might be expected to occur off Australia as well (see Pietsch, 1974, and Pietsch and Seigel, 1980):

- Danaphryne nigrifilis* Regan and Trewavas, 1932
- Microlophichthys microlophus* Regan, 1925
- Chirophryne xenolophus* Regan and Trewavas, 1932
- Pentherichthys* sp.
- Lophodolos indicus* Lloyd, 1909

Family THAUMATICHTHYIDAE

Diagnosis. Females are distinguished from those of other ceratioid families by having upper jaw extending far beyond lower jaw, anteriorly separated, only connected by an elastic membrane; long, hooked premaxillary teeth and 1–3 hooked denticles on esca.

Two genera, *Lasiognathus* and *Thaumatichthys*.

Males only known in the latter genus; distinct from males of other families by having 4 separate, hooked denticles arranged in two pairs above each other on tip of snout and 7 denticles arranged in two transverse series on tip of lower jaw; dermal spines present on body.

No member of the family Thaumatichthyidae has been recorded from Australia. The holotype of *Thaumatichthys pagidostomus* (USNM 72952), however, was collected in adjacent south-east Asian waters off Sulawesi, Celebes (Smith and Radcliffe, 1912); for a complete review see Bertelsen and Struhsaker, 1977.

Family CENTROPHRYNIDAE

Diagnosis. Females are distinguished from those of other ceratioid families by the following combination of characters: opercle bifurcate; suboperculum with anterior spine (reduced in large specimens); four pectoral radials (fusing to 3 in specimens larger than 150 mm); hyomandibular with double head gill teeth present on epibranchial I and ceratobranchials I–IV; esca with a laterally compressed fan-shaped appendage; esca filaments absent. Larvae, males and juvenile females with a short, simple hyoid barbel.

Males probably non-parasitic; upper denticular with 3 teeth, the lower with 4; eyes lateral, less than 5% SL in diameter; anterior nostrils opening anteriorly; skin naked.

A single genus.

No member of the Centrophrynidae has been recorded from eastern Australia. The lectotype of *Centrophryne spinulosa* (ZMUC P92122), however, was captured off the northern coast of New Guinea (Regan and Trewavas, 1932); for a complete review see Pietsch, 1972a.

Family CERATIIDAE

Diagnosis. Females are distinguished from those of other ceratioid families in having two or three caruncles on the dorsal midline just anterior to the soft dorsal fin; sphenotic spines absent; posterior end of pterygiophore of illicium emerging from the dorsal midline anterior to caruncles; cleft of mouth vertical to strongly oblique; skin covered with close-set dermal spines; D.4–5; A.4–5.

Males parasitic; free-living stages with a pair of large denticular teeth on snout, fused at base and articulating with pterygiophore of illicium; two pairs of denticular teeth on tip of lower jaw; eyes large, bowl-shaped; olfactory organs minute.

Two monotypic genera.

Key to Females of Genera and Species of Ceratiidae

1. Illicium long, much longer than bulb of esca;
2 caruncles on dorsal midline; subopercle without spine on anterior margin *Ceratias holboelli* Kröyer, 1845, p.89
- Illicium short, nearly completely enveloped by bulb of esca; 3 caruncles on dorsal midline; subopercle with spine on anterior margin *Cryptopsaras couesi* Gill, 1883, p.91

Key to Males of Genera and Species of Ceratiidae

1. Body without subdermal pigment *Ceratias holboelli* Kröyer, 1845, p.89
- Body with subdermal pigment on gill-cover, back and caudal peduncle *Cryptopsaras couesi* Gill, 1883, p.91

Ceratias Kröyer, 1845

For synonymy see Bertelsen, 1951.

Diagnosis. Females are distinguished from those of *Cryptopsaras* in having two club-shaped caruncles on the dorsal midline just anterior to the soft dorsal fin (minute in specimens greater than 400 mm SL); illicium long, 19–25% of SL.

Males are distinguished by having two pairs of lower denticular teeth of nearly equal size. Larvae, males and juvenile females without subdermal pigment.

A single species (but see comments below).

Ceratias holboelli Kröyer, 1845

Fig. 10

Ceratias holboelli Kröyer, 1845: 638 (original description, single specimen from southern Greenland, holotype ZMUC P61).—Bertelsen, 1951:133–318, figs 90–92 (revision based on all known material).

For complete synonymy see Bertelsen, 1951.

Material. Five metamorphosed females, 22–570 mm SL: AMS I.19562–042, 22 mm SL, E of Port Hacking, N.S.W., 34°09'S, 152°07'E, 0–550 m over 1890 m, 23 March 1971. AMS I.20307–014, 2 (135–168 mm SL), E of Broken Bay, N.S.W., 33°28'S, 152°25'E, 0–900 m over 1830–2800 m, 13

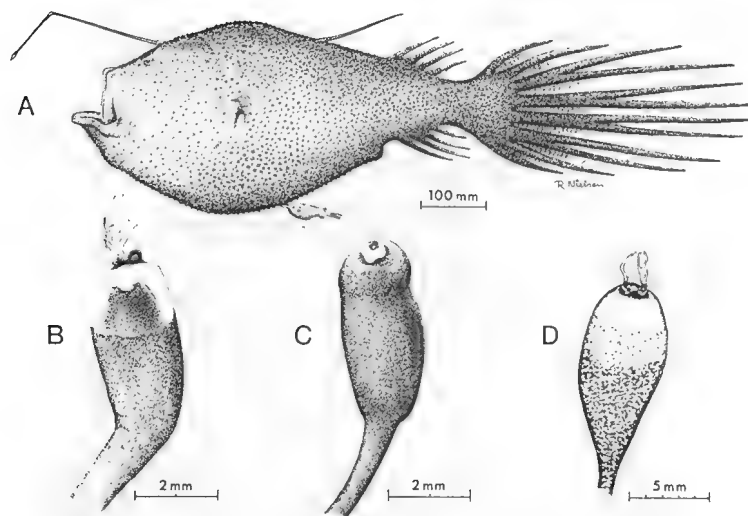


Fig. 10. *Ceratias holboelli* Kröyer, 1845. A, female c.650 mm SL, with parasitic male c.80 mm SL. After Bertelsen (1951). B–D, escae: B, left lateral view, 168 mm SL, AMS I.20307–014, drawn by R. Nielsen. C, posterior view, 135 mm SL, AMS I.20307–014, drawn by R. Nielsen. D, left lateral view, 340 mm SL, BMNH 1949, 11.3.2, after Clarke (1950).

December 1977. WAM P4266, 480 mm SL, 35°34'S, 117°36'E, from stomach of sperm whale, 31 August 1957. WAM P27143–001, 570 mm SL, 35°24'S, 118°30'E, from stomach of sperm whale, 22 September 1964.

Ceratias holboelli has broad distribution in all three major oceans of the world. The holotype of *Mancalias bifilis* Regan and Trewavas, 1932 (referred to *C. holboelli* by Bertelsen, 1951) was collected east of New Zealand (46°43'S, 176°09'E). More recently 14 juvenile females were collected in the Banda, Celebes, Ceram and Halmahera seas (Pietsch and Seigel, 1980). With the exception of the large female (480 mm, WAM P4266) reported by Bowen (1963) and a single larval specimen (5 mm total length, ZMUC P921185) collected at approximately 29°37.5'S, 156°46'E (Bertelsen, 1951:271), the four specimens recorded here are the first from Australian waters.

As noted by Bowen (1963) the esca of the 480 mm SL specimen is damaged and in the 570 mm SL specimen (WAM P27143–001) the illicium is lost. In both of these adult females the skin of the body is complete and shows no sign of male attachment. Both have immature but relatively large ovaries measuring in the 480 mm SL specimen (left ovary) 80 mm in length and 25 mm in width with oocysts of about 0.2 mm in diameter. In the 570 mm SL specimen the respective measurements are 100 × 60 mm with oocysts of 0.2–0.3 mm.

In the smallest (22 mm SL) of the three specimens in the collection of the Australian Museum illicium and esca are damaged.

In the 135 mm SL specimen the illicium measures 17.5% SL, the exerted portion of the pterygiophore, 70% of SL. The esca bulb is oval in shape, pigmented except at the distal tip, and terminates without filaments and without any elevation of the small pigment spot that

surrounds the esca pore. A slight constriction of the bulb below the distally placed photophore may be due to shrinkage in preservation (Fig. 10C).

In the 168 mm SL specimen the length of the illicium is 31% of SL, the total length of the pterygiophore of the illicium is 113% of SL. The esca bulb is somewhat pear-shaped, the proximal two-thirds darkly pigmented. The esca pore is raised on a pigmented tube. A stout filament is present just anterior to the esca pore, its length approximately 75% of the diameter of the esca bulb, bearing three short filaments on each side (Fig. 10A).

Since Kröyer's (1845) original description, material of this genus has been described under nine generic and 13 specific names. More recently (Clarke, 1950; Bertelsen, 1951; Penrith, 1967), however, only the type species has been recognized, but doubt remains as to whether the existing material represents one or more species. Bertelsen (1951:133) found no esca filaments in specimens less than about 75 mm SL. However, in the relatively few larger specimens available with well-preserved escae, those from the North Atlantic (four specimens) had a single distal esca filament, while those from the southern hemisphere (three specimens) had a pair of distal filaments (Fig. 10D). For this reason, Bertelsen (1951) recommended that until further material becomes available, two subspecies should be recognized: a northern *Ceratias h. holboelli* and a southern *Ceratias h. tentaculatus*. Penrith (1967:185) reported a specimen with a distal pair of esca filaments from off Cape Town, and although additional material now available to us (Bertelsen and Pietsch, manuscript) seems to further confirm the existence of a separate southern species, some uncertainty remains. The additional material described here provides nothing to reduce this uncertainty.

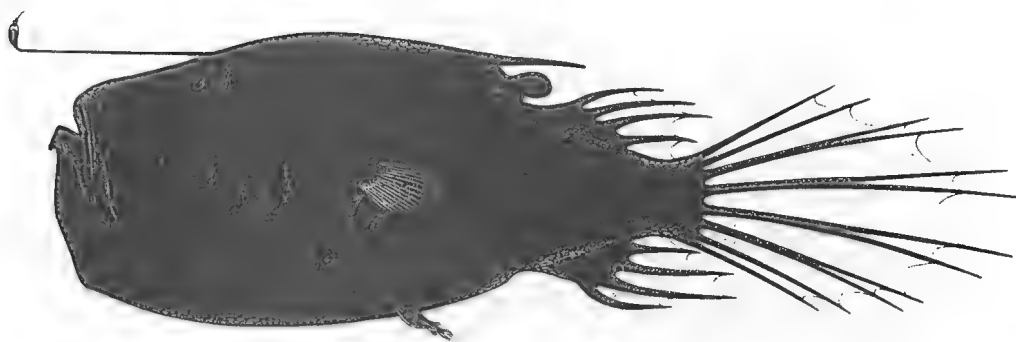


Fig. 11. *Cryptopsaras couesi* Gill, 1883, 290 mm SL. Redrawn after Tanaka (1911).

If *Ceratias tentaculatus* (originally described by Norman, 1930, from a single specimen collected from the Atlantic sector of the Southern Ocean) is resurrected and its distribution shown to be restricted by the Subtropical Convergence, there is still a question as to whether the remaining material from other parts of the world represents one or two species. The 168 mm SL specimen described here with a single esca filament, apparently a typical specimen of *C. holboelli* from eastern Australian waters, indicates a worldwide distribution for this species. On the other hand, additional material is needed to show whether the 135 mm specimen without an esca filament represents merely intraspecific variation or an additional third species.

Cryptopsaras Gill, 1883

For synonymy see Bertelsen, 1951.

Diagnosis. Females are distinguished from those of *Ceratias* in having three club-shaped caruncles on the dorsal midline just anterior to the soft dorsal fin; illicium extremely short, nearly completely enveloped by the esca bulb.

Males are distinguished by having two pairs of lower denticular teeth, the posterior pair considerably shorter than the anterior pair; subdermal pigment present on gill-cover, back and caudal peduncle.

A single species.

Cryptopsaras couesi Gill, 1883

Fig 11

Cryptopsaras couesi Gill, 1883:284 (original description, single specimen from off Long Island, New York, holotype USNM 33558).—Bertelsen, 1951:139-145, figs 93-97, table 29 (review based on all known material).

For complete synonymy see Bertelsen, 1951.

Material. Four females, 8-152 mm SL: AMS I.19601-037, 8 mm SL, E of Sydney, N.S.W., 34°10'S, 151°59'E, 0-75 m over 1810-2470 m, 24 March 1971. AMS I.19608-021, 9 mm SL, off Sydney, N.S.W., 34°05'S, 151°56'E, 0-800 m over 2410-2920 m, 23 March 1971. AMS I.20305-002, 73 mm SL, E of Broken Bay, N.S.W., 33°33'S, 152°18'E, 0-170 m over

2000 m, 12 December 1977. AMS I.20410-008, 152 mm SL, E of Wollongong, N.S.W., 34°27'S, 151°38'E, 0-600 m over 2000-2200 m, 23 May 1978.

Cryptopsaras couesi has a cosmopolitan distribution in all three major oceans of the world (Bertelsen, 1951). Three females from localities off New Zealand and in the Tasman Sea were described by Regan and Trewavas (1932:8). Bertelsen (1951:272) recorded 12 larvae and three free-living, metamorphosed males from eastern Australian waters, in addition to a number of specimens from adjacent south-east Asian waters. An 11 mm SL female collected off Western Australia in 1965 (no other data available) is present in the collections of the Western Australian Museum, Perth (WAM P26831-001). Finally, 50 specimens of this species were reported by Pietsch and Seigel (1980) from collections made in the Banda, Celebes, Halmahera, Sulu and Timor Seas.

Family GIGANTACTINIDAE

Diagnosis. Females are distinguished from those of other ceratioid families by having an elongate body, head less than 35% of SL, caudal peduncle length greater than 20% of SL; sphenotic spines absent; caudal fin with nine rays, but ventralmost ray reduced and embedded giving the appearance of only eight rays; five pectoral radials; skin spinulose.

Males non-parasitic with eyes minute; olfactory organs large; anterior nostrils close together and opening anteriorly; denticular teeth all or nearly all mutually free; upper denticular teeth 3-6 (rarely 2), not connected to pterygiophore of illicium; lower denticular teeth 4-7 (rarely 3).

Two genera, one recorded from eastern Australian waters.

Gigantactis Brauer, 1902

For synonymy see Bertelsen *et al.*, 1981.

Diagnosis. Females are distinguished from those of *Rhynchactis* (the only other genus of the family) in having the lower jaw teeth well developed in several series; D.5-9 (rarely 4 or 10); A.4-7 (rarely 8); esca bulb present.

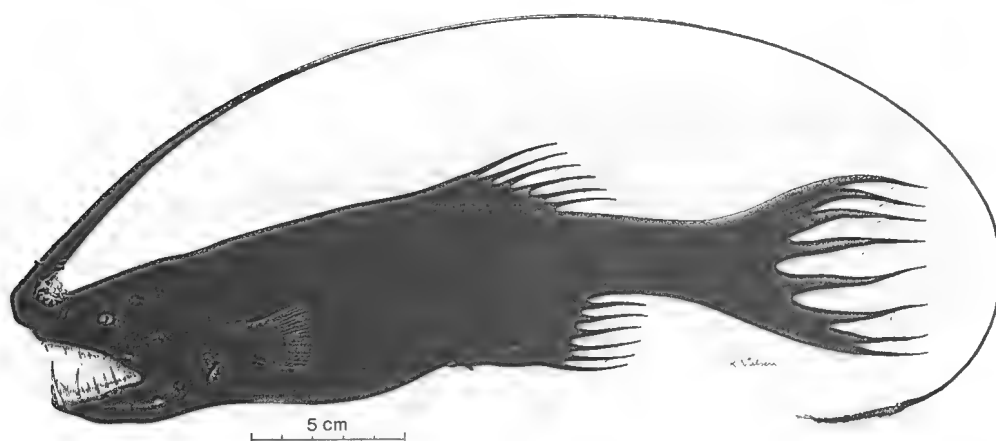


Fig. 12. *Gigantactis paxtoni* Bertelsen, Pietsch and Lavenberg, 1980, holotype, 232 mm SL, AMS I.20314-018, after Bertelsen *et al.* (1980).

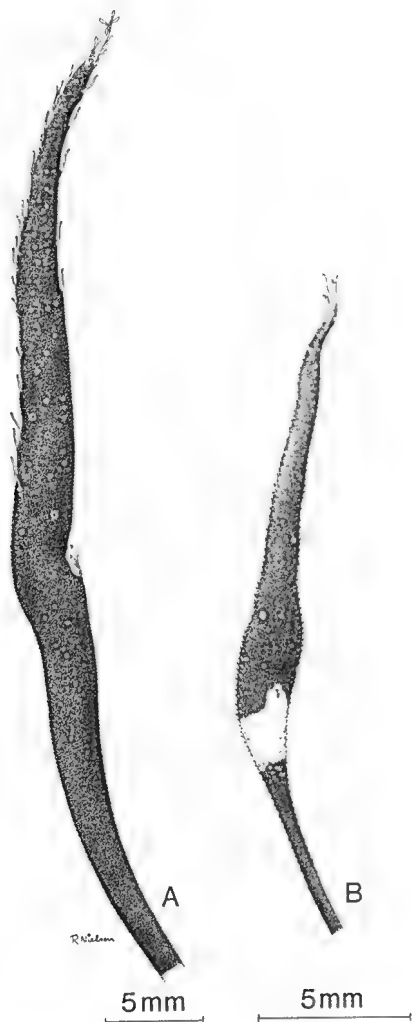


Fig. 13. *Gigantactis paxtoni* Bertelsen, Pietsch and Lavenberg, 1980. Escae: A, left lateral view, holotype, 232 mm SL, AMS I.20314-018; B, Left posterolateral view, paratype, 50 mm SL, IOAN uncatalogued. After Bertelsen *et al.* (1980).

Males are distinguished from those of *Rhynchactis* in having upper denticular teeth 3, lower denticular teeth 4; D.5-9 (rarely 4 or 10); A.4-7 (rarely 8); skin spinulose in some species.

Seventeen species, only one recorded from Australia (Bertelsen *et al.*, 1981), in addition to three *Gigantactis* larvae not identifiable to species (ZMUC P921628-921629, Bertelsen, 1951:274).

Gigantactis paxtoni Bertelsen, Pietsch
and Lavenberg, 1981
Figs 12, 13

Gigantactis "sp.1" Parin *et al.*, 1977:156 (single specimen).
Gigantactis paxtoni Bertelsen, Pietsch and Lavenberg
1981:39-41, figs 36, 37, 38, 64, tables 1, 2, 9 (original
description, eight specimens. Holotype AMS I.20314-018,
232 mm SL).

Material. Seven metamorphosed females 50-232 mm SL:
AMS I.20070-016, paratype, 124 mm SL, NE of Cape Howe,
N.S.W., 37°24'S, 150°30'E, 0-540 m over 3600 m, 1
November 1977. AMS I.20306-007, paratype, 142 mm SL,
65 km E of Broken Bay, N.S.W., 33°31'S, 152°20'E,
0-900 m over 1800-2900 m, 12 December 1977. AMS
I.20314-018, holotype, 232 mm SL; 100 km E of Broken Bay,
N.S.W., 33°28'S, 152°33'E, 0-900 m over 4200 m, 14
December 1977. AMS I.20314-060, 2 paratypes, 218-228 mm
SL, same data as holotype. AMS I.21365-007, 134 mm SL,
off Newcastle, N.S.W., 33°09'S, 153°05'E, 0-750 m over
1500 m, 28 November 1979. ZMUC P921988, paratype,
175 mm SL, same data as holotype.

The original description of *G. paxtoni* was based on
8 metamorphosed females, 6 from the south-east coast
of Australia, one from the north-west coast of New
Guinea and one from western South Indian Ocean. In
addition to the holotype and paratypes listed above, one
female, 134 mm SL (AMS I.21365-007) has been
obtained. The characters of this new specimen are in
full agreement with those of the type material.

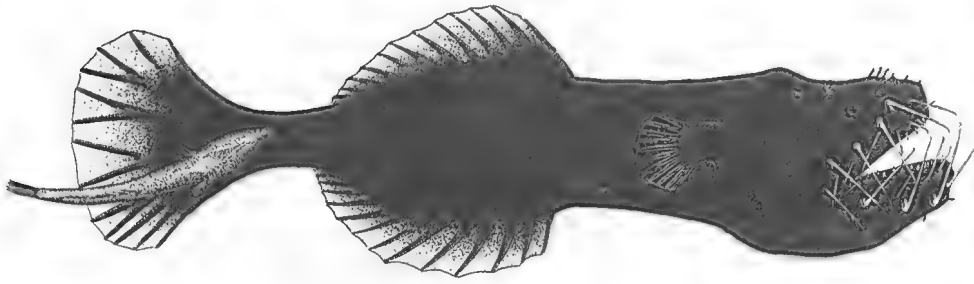


Fig. 14. *Neoceratias spinifer* Pappenheim, 1914, female, 52 mm SL, with parasitic male, 15.5 mm SL, ZMUC P921726. After Bertelsen (1951).

Comments. The closely related species, *Gigantactis vanhoefeni*, is well represented in adjacent Indonesian waters; seven females were recently collected in the Banda Sea (Pietsch and Seigel, 1980). Its presence off Australia is thus a distinct possibility.

Family NEOCERATHIDAE

Diagnosis. Females are distinguished from those of other ceratioid families by the absence of the illicium and esca; body elongate, head less than 30% of SL; a large nasal papilla on each side of snout; long, hooked teeth situated outside of the mouth, movably attached to conical, bony outgrowths of the jaws; caudal fin broad, fan-shaped; skin naked; D.11–13; A.10–13.

Males are parasitic with no upper denticular; lower denticular with three projections each ending in a double hook (Bertelsen, 1951:161, fig. 105B); eyes and olfactory organs degenerate; skin naked. Free-living stages unknown.

A single genus.

Neoceratias Pappenheim, 1914

With the characters of the family.

A single species.

Neoceratias spinifer Pappenheim, 1914

Figs 14, 15

Neoceratias spinifer Pappenheim, 1914:198, fig. 10 (original description, single specimen from the south Atlantic at approximately 12°11'S, 6°16'W, holotype ZMB 19383).—Bertelsen, 1951:158–161, figs 105, 106, tables 35, 36 (review based on all known material, osteology, parasitic male and larvae); Pietsch, 1976:789, fig. 8 (additional material, reproduction).

With the characters of the family.

Material. AMS I.20908–002, a female (77 mm SL) with parasitic male (12.5 mm SL), off Cape York Peninsula, Queensland, 14°30'S, 145°42'E, Tucker trawl, 0–1200 m, 1 February 1979, R/V 'Lady Basten'.

The number of known specimens of this species has now been brought to 28. Eleven of these are larvae and

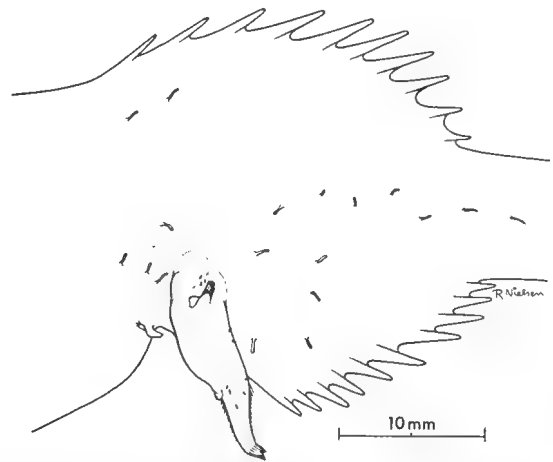


Fig. 15. *Neoceratias spinifer* Pappenheim, 1914, parasitic male, 12.5 mm SL, with head partly embedded in body of female, 77 mm SL, AMS I.20908–002. Drawn by R. Nielsen.

12 are metamorphosed females (17–108.5 mm SL), five of which carry a single parasitic male (Bertelsen, 1951; Pietsch, 1976). Although this material comes from widely scattered localities in the warmer latitudes of the Atlantic, Indian and Pacific oceans, the parasitized female reported here is the first record from Australia.

The specimen in the collections of the Australian Museum agrees in all respects with the description provided by Bertelsen (1951). The ovaries are approximately 11 mm (about 14% of SL) in length and contain numerous immature eggs, the largest of which measures approximately 0.15 mm in diameter. The male is attached anteriorly on the left side of the base of the anal fin (Fig. 15). The testes are large. The head is nearly completely embedded in the tissue of the female with the mouth fully occluded. Two of the four previously described parasitic males of *Neoceratias* have similarly closed mouth openings, in contrast to all the approximately 60 known cases of parasitism in other certaoid species. In these, more or less distinct lateral openings remain at the corners of the mouth that perhaps permit a normal direction of the respiratory current. Since the gills of the *Neoceratias* males with

occluded mouths are normally developed, it may be assumed that water for respiration is pumped in and out through the opercular opening (Pietsch, 1976:790).

Family LINOPHRYNIDAE

Diagnosis. Females are distinguished from those of other ceratioid families in having 3 (very rarely 2 or 4) dorsal and anal fin rays; skin naked; anus sinistral, 5 branchiostegal rays.

Males become parasitic; free-living stages with eyes large, somewhat tubular, and more or less directed anteriorly.

Five genera (see Bertelsen, 1951), two recorded from Australian waters.

Key to Females of Genera of Linophrynidae Recorded from Australian Waters

1. Skin darkly pigmented, opaque; hyoid barbel present; teeth few and strong *Linophryne*
- Skin unpigmented, transparent; hyoid barbel absent; teeth small, numerous *Haplophryne*

Key to Males of Genera of Linophrynidae Recorded from Australian Waters

1. Skin pigmented; denticular teeth strong; pre-maxillae and larval teeth degenerating with growth *Linophryne*
- Skin unpigmented; denticular teeth weak; pre-maxillae and larval teeth retained with growth *Haplophryne*

Linophryne Collett, 1886

For synonymy see Bertelsen, 1951 and 1982.

Diagnosis. Females are distinguished from those of other linophrynid genera in having a well-developed hyoid barbel, bearing small, globular photophores; gape of mouth large with few teeth, some of which are extremely long; sphenotic spines well developed; preopercular spine simple.

Free-living males with skin darkly pigmented; subdermal pigment present; premaxillae degenerate; jaw teeth few to absent; upper and lower denticular teeth well developed.

Twenty-one species (Bertelsen, 1982), only one recorded from Australian waters (plus one poorly preserved and unidentifiable specimen).

Linophryne densiramus Imai, 1941 Fig. 16

Linophryne densiramus Imai, 1941:247–250, figs 14–17, table 7 (original description, single specimen from Japan, holotype uncatalogued).—Bertelsen, 1980: 55–59, figs 11, 12, 17, tables 1, 2, 4 (resurrection from synonymy of *Linophryne arborifera*, 12 new records).

Linophryne arborifera.—Bertelsen, 1951: 178–183 (in part; *Linophryne densiramus* regarded as a synonym); Parin

et al., 1977: (in part; additional specimen from the Banda Sea; misidentification after Bertelsen, 1951).

Material. AMS I.20314–015, 42 mm SL, 100 km E of Broken Bay, N.S.W., 33°28'S, 152°33'E, 0–900 m over 4200 m, 14 December 1977.

Fourteen females of *Linophryne densiramus* are known, one of them with a parasitic male. They were collected from scattered localities in the western Atlantic, Gulf of Mexico, Banda Sea and Pacific Ocean. The Australian Museum specimen (Bertelsen, 1980:58, fig. 12H) is the first record from the Australian coast; it is in full agreement with the specimens from other areas.

Linophryne sp.

Material. AMS I.20070–006, 24 mm SL, NE of Cape Howe, N.S.W., 37°24'S, 150°30'E, 0–540 m over 3600 m, 1 November 1977.

Specific identification of this specimen is impossible because of the loss of both the esca and barbel. By means of other morphological characters, however, a number of the recognized species of the genus can be excluded. According to subdermal pigmentation it does not represent *L. densiramus*, but most probably *Linophryne* subgenus *Linophryne* Bertelsen, 1982.

Other Species of *Linophryne*

Two additional species of *Linophryne* were recently collected in nearby Indonesian waters (Bertelsen, 1978, 1981, Pietsch and Seigel, 1980). These are *Linophryne indica* (Brauer, 1902) and *Linophryne trewavasae* Bertelsen, 1978. Either one or both of these forms might be expected to occur in Australian waters as well.

The *Aceratias indicus* recorded from Australian waters by Regan and Trewavas (1932) and Whitley (1964) is based upon male *Linophryne* unidentifiable to species.

Haplophryne Regan, 1912

For synonymy see Bertelsen, 1951 and Munk and Bertelsen, 1983.

Diagnosis. Females are distinguished from those of other linophrynid genera by the absence of a hyoid barbel; numerous, relatively small jaw teeth in 3–4 rows; large frontal spines present; preopercle with a large compressed spine terminating in 2–5 radiating cusps; esca sessile on snout; skin naked without pigment.

Males parasitic; free-living stages with well-developed jaw teeth; denticular teeth feeble; skin unpigmented. A single species.

Haplophryne mollis (Brauer, 1902) Figs 17–18

Aceratias mollis Brauer, figs 17, 18 (original description, single male from Indian Ocean, holotype ZMB 17713).

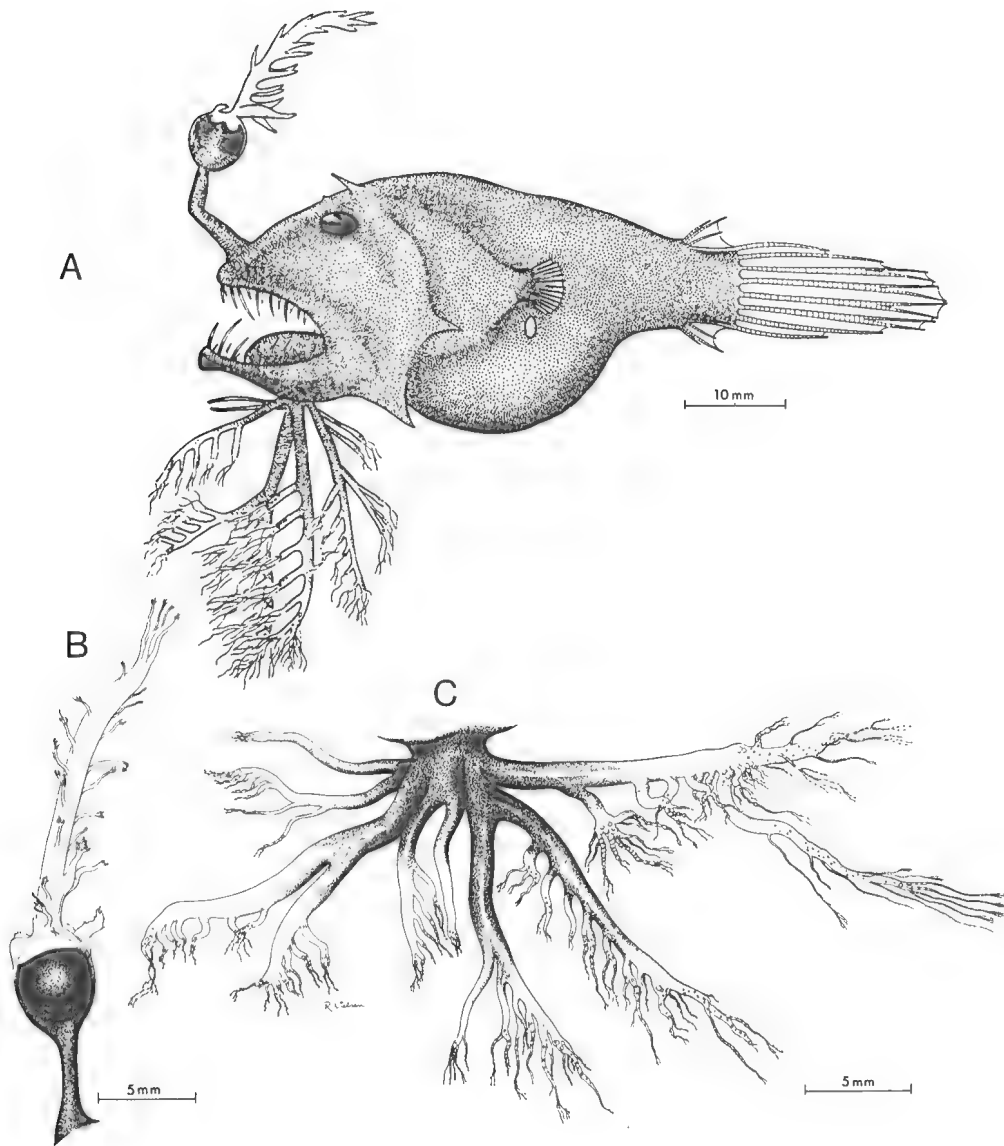


Fig. 16. *Linophryne densiramus* Imai, 1941. A, holotype, 50 mm SL, after Imai, 1941. B, and C, left lateral view of esca and barbel, 43.5 mm SL, LACM 38440-1. After Bertelsen (1980).

Haplophryne mollis.—Regan, 1912:289 (gen. nov.); Munk and Bertelsen, 1982: (*Haplophryne mollis* (Brauer, 1902), a senior synonym for *Edriolychnus schmidtii* Regan, 1925). *Edriolychnus schmidtii* Regan, 1925:398, figs 8, 9 (original description, single specimen, parasitized female from the Caribbean Sea, holotype ZMUC P92135).—Bertelsen, 1951:168–172, figs 111A, B, 112–115, tables 38–40 (revision based on all known material).
For additional synonymy see Bertelsen, 1951.
With the characters of the genus.

Material. Seven females (29–62 mm SL), five (39–62 mm SL) with parasitic males (10.5–15 mm SL): AMS I.20070–002, 32 mm SL, NE of Cape Howe, N.S.W., 37°24'S, 150°30'E, 0–540 m over 3600 m, 1 November 1977. AMS I.20071–001, female (52.5 mm SL) with 2 parasitic males (11.5–12 mm SL), E of Kiama, N.S.W., 34°40'S, 151°15'E, 0–548 m over 3300 m, 3 November 1977. AMS I.20314–014, 2 females

(29 mm SL without male; 46 mm SL with parasitic male, 11 mm SL), 100 km E of Broken Bay, N.S.W., 33°28'S, 152°33'E, 0–900 m over 4200 m, 14 December 1977. AMS I.20315–009, female (39 mm SL) with parasitic male (12.5 mm SL), 65 km E of Sydney, N.S.W., 33°53'S, 152°02'E, 0–900 m over 1800 m, 14 December 1977. AMS I.21364–003, female (48 mm SL) with 2 parasitic males (10.5–12 mm SL), off Newcastle, N.S.W., 33°01'S, 153°01'E, 0–750 m over +1500 m, 27 November 1979. AMS I.21365–008, female (62 mm SL) with 2 parasitic males (12–15 mm SL), off Newcastle, N.S.W., 33°09'S, 153°05'E, 0–750 m over +1500 m, 28 November 1979.

A total of approximately 35 females and free-living males have been reported from scattered positions in the warmer latitudes of all major oceans. The material recorded here constitutes the first occurrence of this species in Australian waters.

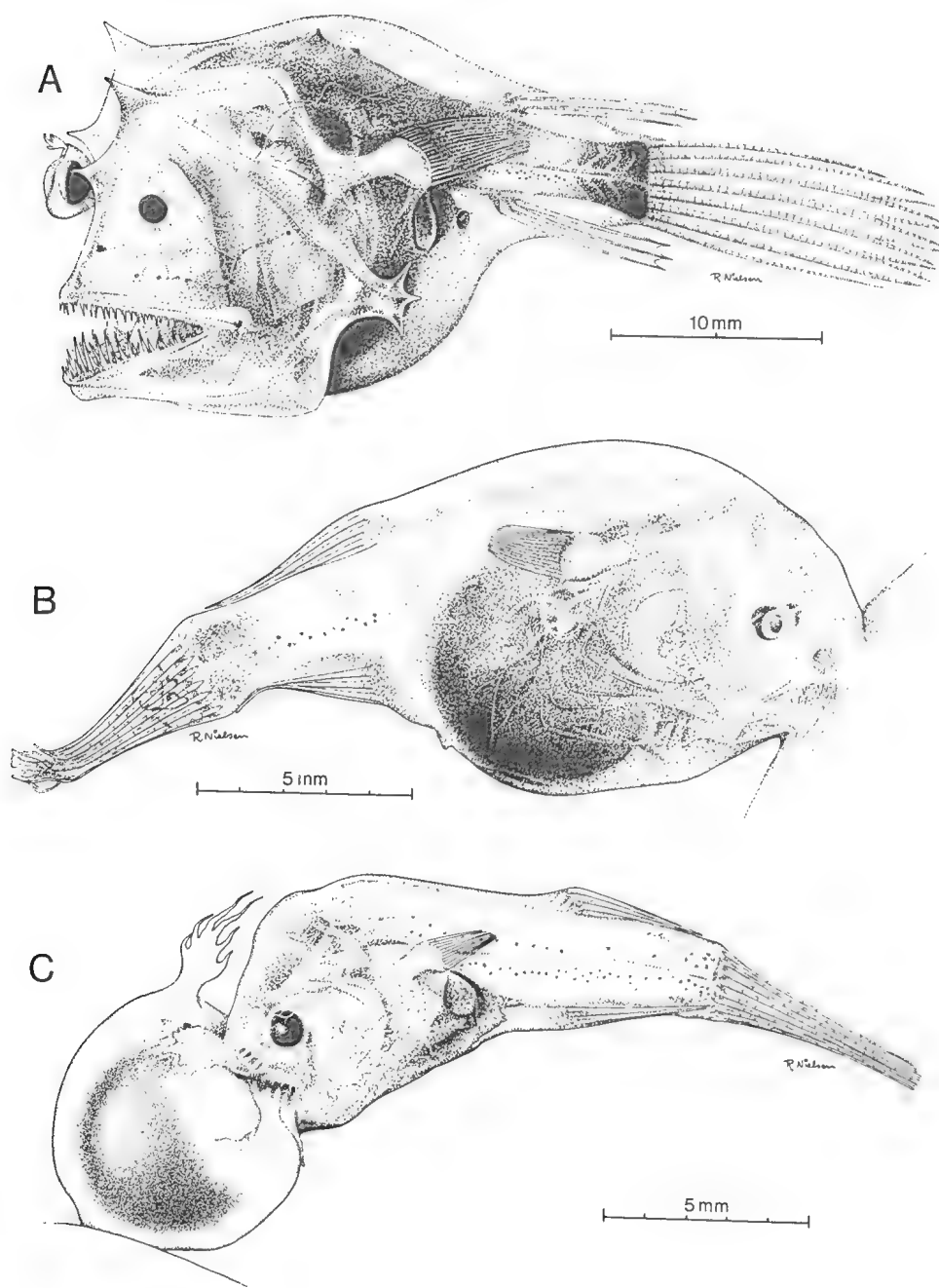


Fig. 17. *Haplophryne mollis* (Brauer, 1902). A, female, 29 mm SL, AMS I.20314-014. B, male, 15 mm SL, parasitically attached to belly of 62 mm SL female, AMS I.21365-008. C, male, 12 mm SL, parasitically attached to the distal surface of the esca of 62 mm SL female, AMS I.21365-008. Drawn by R. Nielsen.

The seven females in the collections of the Australian Museum are very similar and agree in all respects with previous descriptions. As shown by Bertelsen (1951:170-171), the shape of the preopercular spines varies: in four of the specimens both spines are tricuspid; they are broken in AMS I.20070-002; the left is tricuspid while the right has only two cusps in AMS I.21364-003; the left is undivided, the right bicuspid in AMS I.21365-008. The escae, decreasing in diameter from 12 to 10 per cent of SL with increasing standard length,

bear a compressed posterior appendage with 2-6 distal filaments. The skin is totally unpigmented except for a dark spot surrounding the sinistral anus, and a similar pigment spot surrounding the gill opening in the two smallest females (29-32 mm SL). Secondary subdermal pigmentation increased in distribution and density with increasing standard length. In the smallest female (29 mm SL), secondary subdermal pigment covers only the posterior-most myomeres of the caudal peduncle (Fig. 17); in the larger specimens this pigment has spread

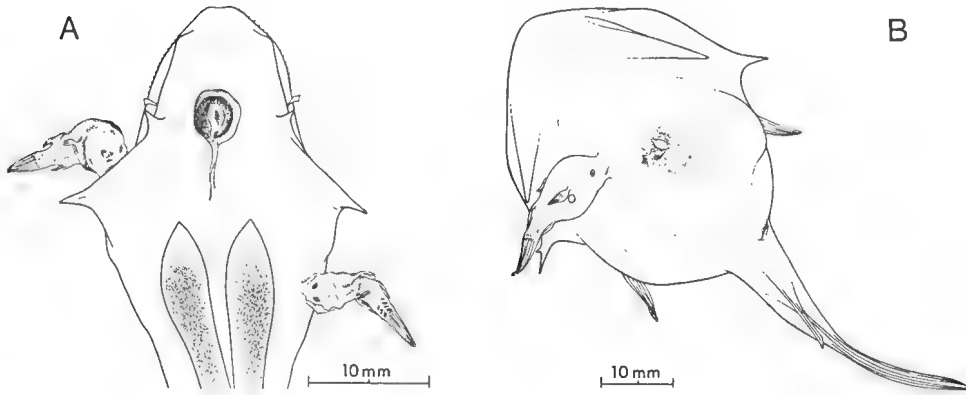


Fig. 18. *Haplophryne mollis* (Brauer, 1902). A, dorsal view of female, 52.5 mm SL, AMS I.20071-001, with two parasitic males, 11.5–12 mm SL. B, ventral view of female, 62 mm SL, AMS I.21365-008, showing parasitic male and scar left by another parasitic male. Drawn by R. Nielsen.

anteriorly, gradually covering the larval series of large melanophores along the sides of the body.

All of the females are immature with small ovaries containing eggs of less than 0.1 mm in diameter.

Five of the seven females are sexually parasitized. The two smaller (29–32 mm) are without males, each of the two next largest (39–46 mm) carries a single male, while each of the three largest females (48–62 mm) has two attached males and an additional scar with remains of the jaw bones of a lost male. The eight males represent somewhat different development stages. Seven of them are of about the same length (10.5–12.5 mm SL) as the largest known free-living *Haplophryne* males, but differ in development of subdermal pigmentation and testes. The 11.5 mm male of AMS I.20071-001 (Fig. 18) and the 12 mm male of AMS I.21365-008 (Fig. 17) appear to be the youngest, having very little secondary subdermal pigment on the caudal peduncle and without any trace of eye degeneration or distinct enlargement of gonads. The 12.5 mm male of AMS I.20315-009 and especially the 15 mm male of AMS I.21365-008 (Fig. 17) are in more advanced stages with secondary pigment completely covering the larval series of large melanophores along the sides of the body, with somewhat shrunken eyes and the belly greatly inflated with enlarged testes. The latter is the first record of a parasitic *Haplophryne* male that is distinctly longer and more voluminous than the largest known free-living males of the genus, thus representing the first evidence of growth based on true parasitism in this genus. In two of the females (AMS I.23364-003 and AMS I.23365-008) the scar, which indicates the position of a lost parasitic male, has a small central papilla and, on each side of this, remains of jaw bones with teeth embedded in the skin. In both specimens numerous radiating blood vessels are distinct in the tissue surrounding the scar. In AMS I.20071-001 the scar is indistinct and only remains of the jaw bones of the male are left. While the scars and three of the parasitic males were placed on the belly of the females, the remaining five males were attached in various places on the head.

Especially remarkable is the position of the smaller male of AMS I.21365-008, attached to the distal surface of esca of the female (Fig. 17).

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The Melitidae of Lizard Island and Adjacent Reefs, The Great Barrier Reef, Australia (Crustacea: Amphipoda)

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ABSTRACT. This paper is the first study of melitid amphipods from tropical Australia. Seventeen species of Melitidae in the genera *Ceradocus*, *Dulichchiella*, *Elasmopus*, *Maera*, *Mallacoota* and *Parelasmpopus* are recorded from Lizard Island and adjacent reefs. In addition *Ceradocus hawaiiensis* Barnard is recorded from Heron Island. Seven new species are described: *Ceradocus oxyodus*, *C. wooree*, *C. yandala*, *Elasmopus crenulatus*, *E. spinicarpus*, *Maera griffini* and *Mallacoota balara*. A lectotype is established and described for *Parelasmpopus suensis*. The diagnosis for the genus *Mallacoota* is expanded and a key to the known species included.

None of the Melitidae from Lizard Island and adjacent reefs has been recorded from southern or south-eastern Australia. Madagascar and Mauritius have the highest number of melitid species in common with the Lizard Island area.

BERENTS, P.B., 1983. The Melitidae of Lizard Island and adjacent reefs, the Great Barrier Reef, Australia (Crustacea: Amphipoda). Records of the Australian Museum 35(3): 101-143.

The Gammaridea of the Great Barrier Reef have not been previously studied. The only published work is that of K.H. Barnard (1931) who reported on the Amphipoda collected by the Great Barrier Reef Expedition conducted by the British Museum in 1928-29. He reported briefly on 14 species from 11 families and the only Melitidae were identified as *Ceradocus rubromaculatus* and *Maera* sp. J.L. Barnard (1976) stressed that little is known of tropical Amphipoda, especially when compared with studies of the group in cold temperate waters.

Recently major collecting programmes with the emphasis on small invertebrates have been carried out by the Australian Museum in the Lizard Island area on the northern Great Barrier Reef. Dr P.A. Hutchings and P.B. Berents sampled reef rock communities (Hutchings and Weate, 1977, 1979). An expedition to sample algal and soft bottom communities was conducted by Dr J.K. Lowry and Dr A.R. Jones. These collections are the basis of this study.

The aim of this study is to record the species of melitid amphipods from Lizard Island and adjacent reefs. New species are described, and for those species already known, the morphology of populations from Lizard Island is compared with other populations described in the literature. The distributions of the species among different habitats and localities in the Lizard Island area are compared. The Melitidae of Lizard Island are

compared with melitid faunas from southern Australia and the Indo-Pacific.

Sampling was carried out at Lizard Island and adjacent reefs, which allowed sampling of the fringing reefs of a high island, a coral cay and outer barrier reefs (Fig.1).

Lizard Island (14°40'S, 145°28'E) lies 18 nautical miles north-east of Cape Flattery on the Queensland coast. It is a high rocky island surrounded by fringing reefs that enclose and protect a shallow lagoon from the prevailing south-east trade winds which blow from March to November. The north-west monsoon affects the region from December to March.

Yonge Reef (14°36'S, 145°38'E) lies 10 nautical miles north-east of Lizard Island. It is part of the chain of shelf edge reefs that follows the continental shelf from the Murray islands (9°58'S) south to approximately 16°S (Orme, 1978). It is a cusped ribbon reef with a backward growth of reef formed by strong currents (Veron, 1978). Behind the reef is a sheltered lagoon-like area with a sandy bottom and scattered bommies known as the reef back. The outer slope at Yonge Reef drops to 40 metres with sand and rubble at the bottom of the slope.

Eagle Islet (14°42'S, 145°23'E) is a coral cay 5 nautical miles south-east of Lizard Island. The reef surrounding Eagle Islet is 2 nautical miles long and 1.5 nautical miles wide.

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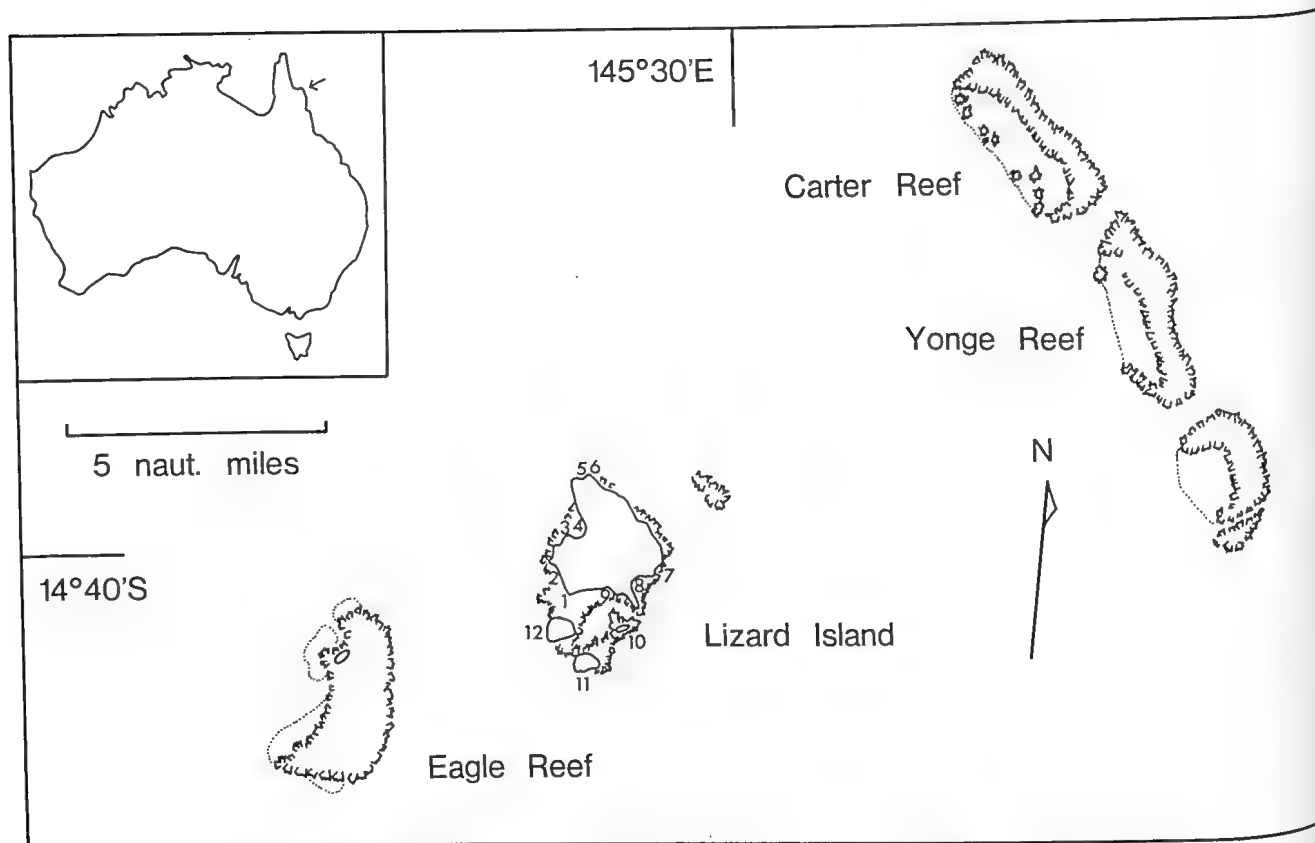


Fig. 1. Map of Lizard Island and adjacent reefs. 1, Station Beach; 2, Casuarina Beach; 3, Chinaman's Head; 4, Watson Bay; 5, Mermaid Cove; 6, North Point; 7, Crystal Beach; 8, Coconut Beach; 9, Mangrove Beach; 10, Bird Islet; 11, South Island; 12, Palfrey Island.

Material from this study has been lodged in the Australian Museum (AM), the United States Museum of Natural History (USNM) and the British Museum (Natural History) (BMNH).

All sublittoral samples were taken using scuba. Collecting techniques varied with the particular habitat being sampled. Sediment samples were collected using an air lift operated from scuba which retained the sediment in a nylon mesh bag. Amphipods were separated from the sediment in an elutriator, in which water was forced through the sediment, allowing the amphipods to float to the surface. The air lift was also used to sample the epifauna of coral heads and gorgonians. Samples of reef rock and dead coral were taken using a hammer and chisel, and immediately placed in a plastic bag and sealed (Hutchings and Weate, 1977, 1979). Samples of algae and seagrasses were placed in fine mesh bags. The fauna from these samples were sorted using a horizontal riffle tray.

The length of the whole animal was measured from the apex of the rostrum to the base of the telson, along the dorsal outline of the body viewed from the lateral aspect. The method described by Barnard and Drummond (1978) was used for measuring dissected parts. The term "mark" as defined by Barnard and Drummond (1978) was used in describing some parts: "Mark (M) followed by a number 0-100 refers to a point on an appendage, article or ramus, the distance from

which point to the base of the structure is expressed as the percentage of the total length of that structure."

The number of specimens examined from each sampling site is stated in brackets following the number of the sampling site. Details of sampling sites are listed in Appendix A.

The following code is used for labelling figures:

H = profile of head

A1 = antenna 1

MP = maxillipeds

MX1 = maxilla 1

MX2 = maxilla 2

MD = mandible

C1-C7 = coxa 1 to coxa 7

G1 = gnathopod 1

G2 = gnathopod 2

P3-P7 = peraeopod 3 to peraeopod 7

D3-D7 = dactylus of peraeopod 3 to dactylus of peraeopod 7 (setae of article 6 not shown)

PLN1-PLN3 = pleonite 1 to pleonite 3

UR1-UR3 = urosomite 1 to urosomite 3

U3 = uropod 3

T = telson

EP3 = third pleonal epimeron

r = right

l = left

n = specimen no. 3

x = specimen no. 4.

Family MELITIDAE Bousfield

Genus *Ceradocus* Costa

Sheard (1939) recorded four species of *Ceradocus* from southern and south-eastern Australia: *C. sellickensis* Sheard, *C. serrata* (Bate), *C. rubromaculatus* (Stimpson) and *C. ramsayi* (Haswell). J.L. Barnard (1972a) also examined collections from southern and south-eastern Australia and described a new species *C. dooliba*. The only species previously recorded from tropical Australia was *C. rubromaculatus* which K.H. Barnard (1931) recorded from Low Isles, Great Barrier Reef. Examination of these specimens in the British Museum (Natural History) showed them to be *Ceradocus oxyodus* n.sp.

Three new species of *Ceradocus* are described from Lizard Island and adjacent reefs. *Ceradocus rubromaculatus* was not found in the material examined. *Ceradocus hawaiiensis* Barnard has not been previously recorded in Australia. Specimens of *C. hawaiiensis* from the southern Great Barrier Reef have recently been deposited in the Australian Museum and are documented herein.

Ceradocus (Denticeradocus) hawaiiensis Barnard, 1955

Fig. 2

Ceradocus hawaiiensis J.L. Barnard 1955: 5-8, figs 2,

3.—1970:115, fig. 65; 1971:70, fig. 41; Ledoyer, 1972: 207-213, figs 30, 31; 1978:266-267.

Material. 14 specimens, AM P30646, Heron Island, Great Barrier Reef (23°26'S, 151°55'E) commensal with the hermit crab *Dardanus megistos*, A.J. Bruce, 11 July 1980.

Diagnosis. Accessory flagellum 6-articulate; coxa 1 anteroventral corner acute; second gnathopods asymmetrical; article 6 of larger second gnathopod with transverse deeply toothed palm; article 2 of pereopods 5-7, posteroventral corner acute; posterior margin of pleonites 1, 2, 3 with 13-17, 10-15, 6-11 dorsal teeth respectively; posterior margin of epimera 1 and 2 entire; epimeron 1 ventral margin may have 1 notch; epimeron 2 ventral margin 1-2 notches; epimeron 3 with 2 notches on ventral margin, 1 tooth on posterior margin; posterior margin of urosomites 1, 2, 3 with 2-3, 2-3, 0 dorsal teeth respectively; telson wider than long, deeply cleft, apices tapering to a point each bearing 2-4 spines.

Remarks. The material examined fits the description of *C. hawaiiensis* from Hawaii (J.L. Barnard 1955, 1970, 1971). The number of dorsal teeth on the posterior margin of pleonite 3 is variable, however, all specimens examined showed 3 curved teeth at each extremity of the dorsal margin. The number of smaller teeth between these 6 teeth is variable.

Distribution. Hawaii (type locality); Madagascar; Mauritius; Heron Island.

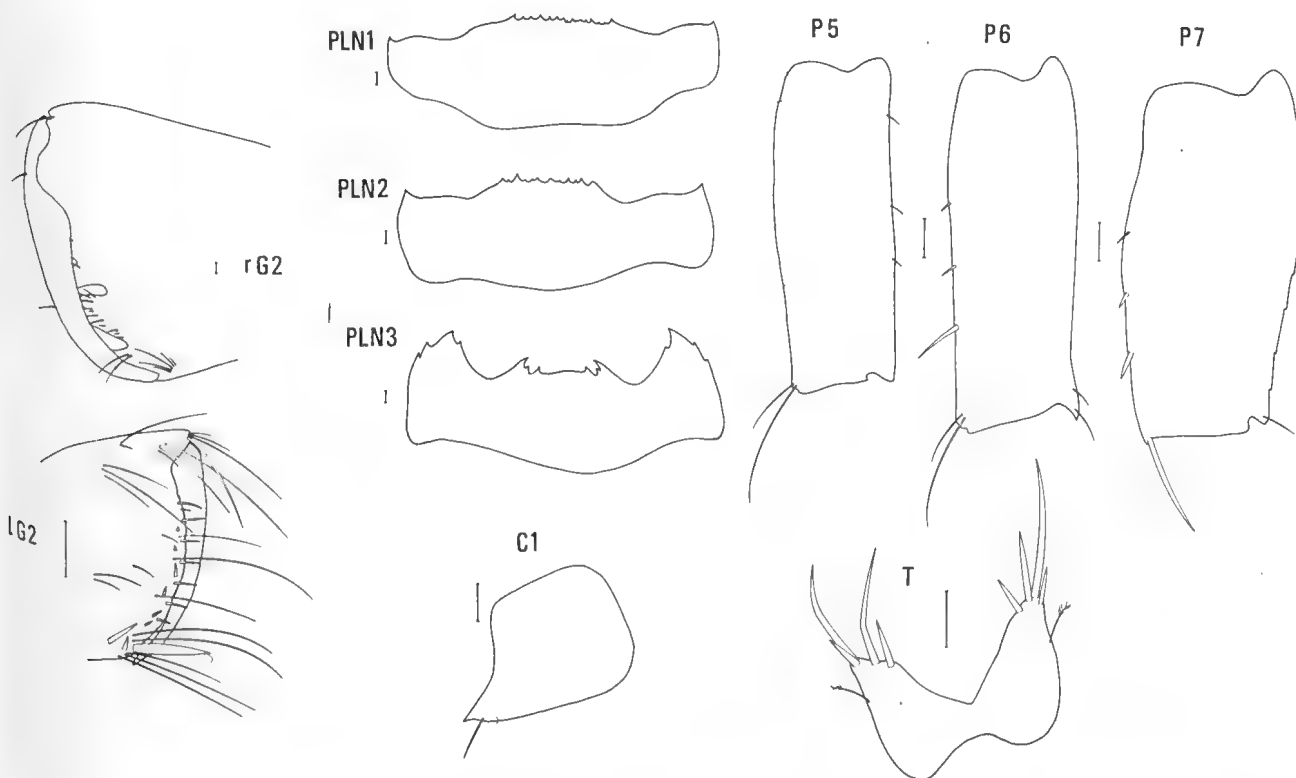


Fig. 2. *Ceradocus hawaiiensis* Barnard, female, 4.8 mm, AM P30646; pleonites 1-3, female, 6.4 mm, AM P30646. Scale lines represent 0.1 mm.

Ceradocus (Denticeradocus) oxyodus n.sp.

Figs 3, 4

Ceradocus rubromaculatus.—K.H. Barnard, 1931:124.

Type material. HOLOTYPE, male, 8.9 mm, AM P31716;
3 PARATYPES, AM P31717, Casuarina Beach, Lizard Island

(14°40.5'S, 145°26.6'E), under stones at low tide mark, J.K. Lowry, A.R. Jones and P.C. Terrill, 11 October 1978, LI-39.

Diagnosis. Accessory flagellum 6-articulate; coxa 1 anteroventral corner acute; second gnathopods symmetrical; palm of second gnathopod oblique, defined by cusp armed with 2 stout spines, palmar

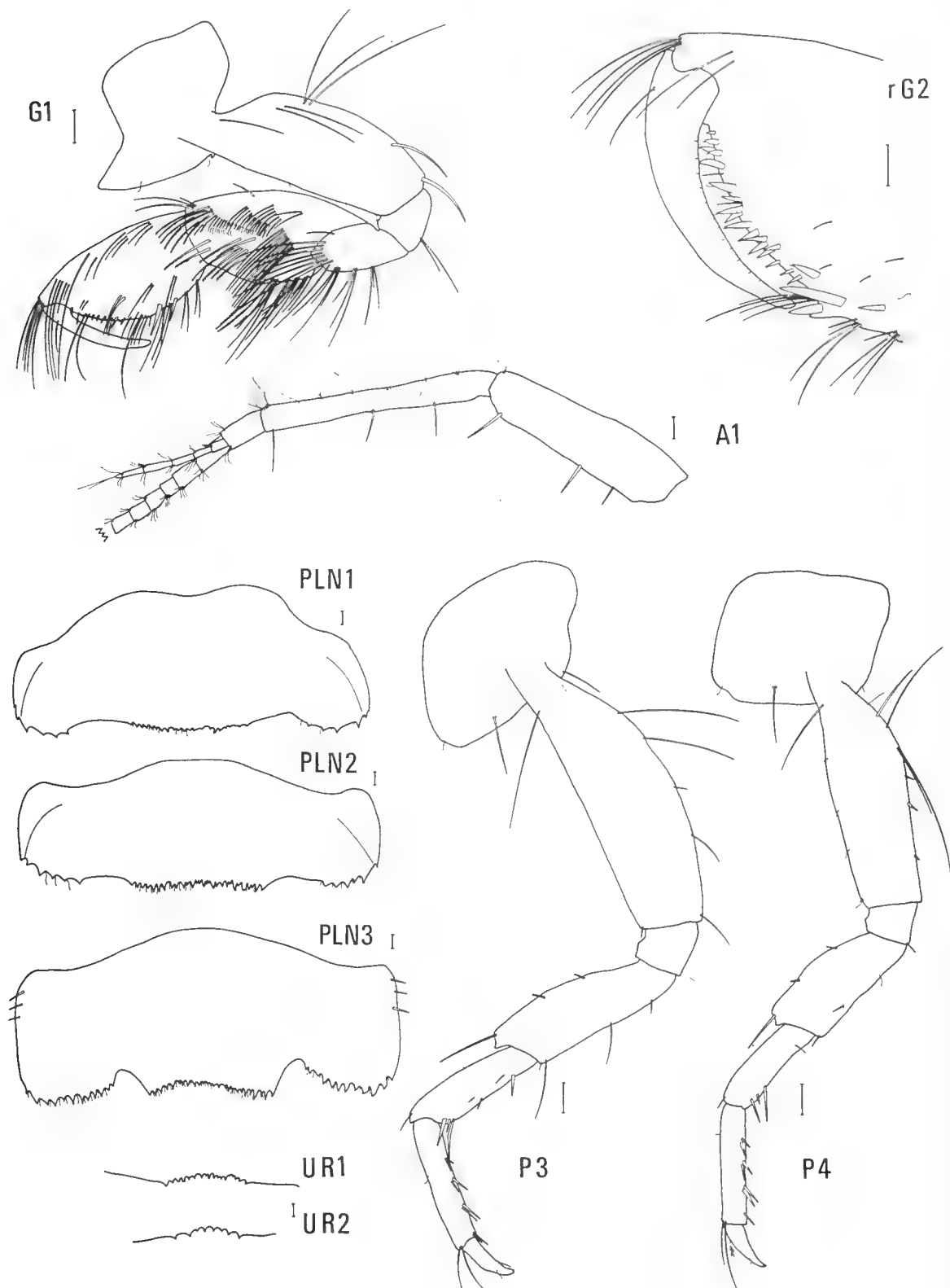


Fig. 3. *Ceradocus oxyodus* n.sp., holotype, male 8.9 mm, LI-39. Scale lines represent 0.1 mm.

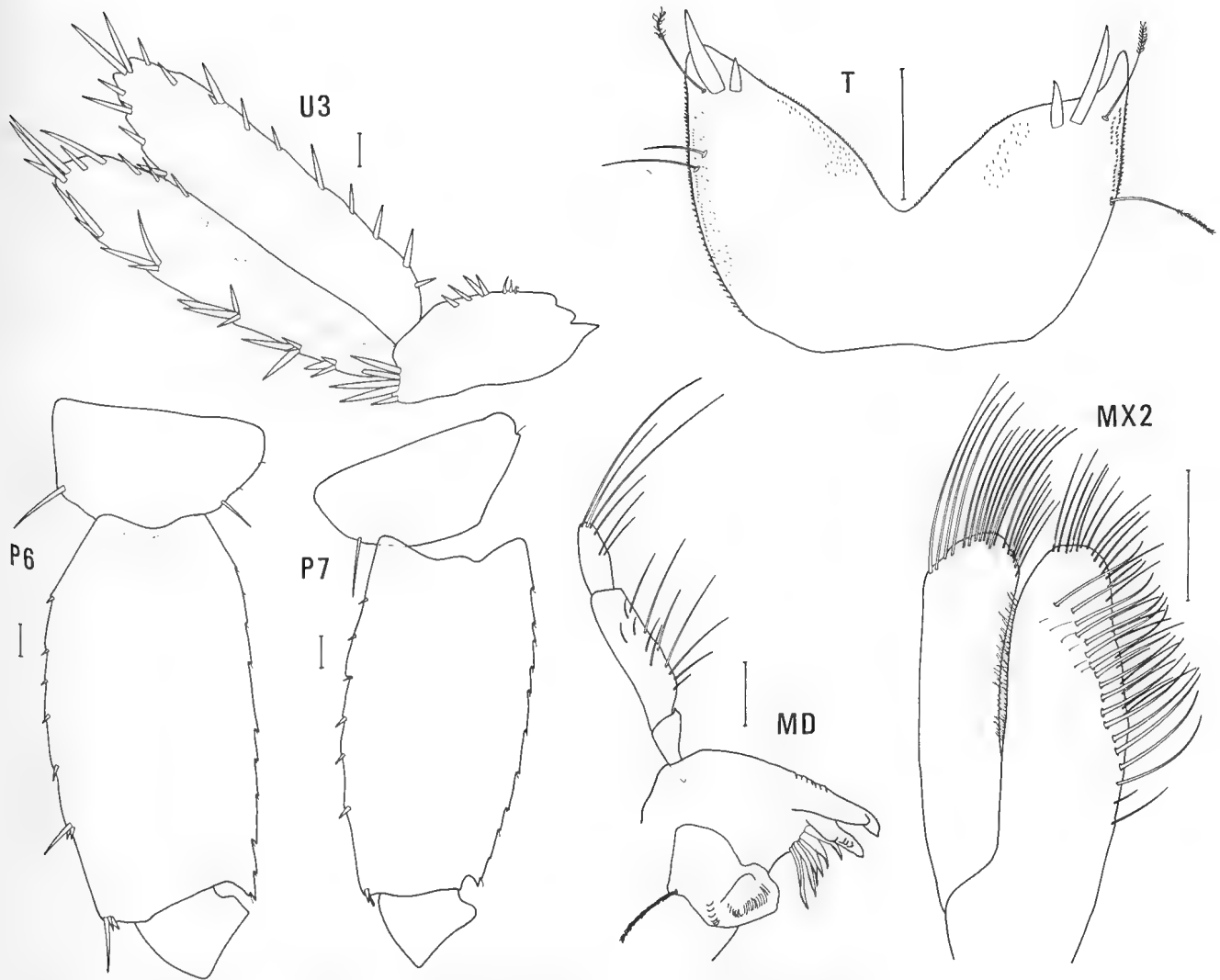


Fig. 4. *Ceradocus oxyodus* n.sp., holotype, male 8.9 mm, LI-39. Scale lines represent 0.1 mm.

margin spinous; article 2 of pereopods 5-7, posteroventral corner acute; posterior margin of pleonites 1, 2, 3 with 14-26, 18-29, 19-26 dorsal teeth respectively; epimeron 1 posterior margin with 4-5 teeth; epimeron 2 posterior margin with 5 teeth; epimeron 3 ventral margin entire, posterior margin bearing 10-12 teeth; posterior margin of urosomites 1, 2 with 8-18, 7-8 dorsal teeth respectively; telson tumid, wider than long, cleft midway to base, apices each bearing 2 spines and plumose seta.

Description. Holotype male, 8.9 mm. *Head* as long as first two pereonites, cheek notch narrow. *Antenna 1*: 1.7 times as long as antenna 2; peduncle and flagellum equal, article 1 armed with 3 ventral spines, article 2 slightly longer than article 1, bearing 3 stout ventral setae, article 3, 0.2 times as long as article 2; flagellum 21-articulate; accessory flagellum 6-articulate, article 6 small, extending to distal margin of article 5 of primary flagellum. *Antenna 2*: peduncle 2.6 times as long as flagellum, gland cone on article 2 extends to M67 on article 3; flagellum 12-articulate.

Mandible with incisor and 7 accessory blades; lacinia mobilis armed with 4 teeth; molar triturating with ragged seta; palp 3-articulate, article 1 equal to article 3, article 2 twice as long as article 1; article 1 with small medial cusp. *Maxilla 1*: inner plate broad with 12 terminal setae; outer plate armed with 9 barbed spine teeth; palp 2-articulate with 12 terminal setae. *Maxilla 2*: plates equal in length, both with terminal setae; inner plate with fine marginal setae, oblique row of medial setae. *Maxillipeds*: inner plate truncate, row of 11 plumose setae from inner margin to apex; outer plate ovate, 16 plumose setae at apex and along inner margin; palp 4-articulate, inner margin of articles 2 and 3 setose.

Gnathopod 1: coxa as long as wide, anterior margin excavate, posteroventral corner notched, anteroventral corner acute; article 2, 0.4 times as wide as long; article 4 anterior and posterior margins converging to a point, distally setose; article 5 subequal to article 6, posterior margin setose, 3 rows superior medial setae with some setae pectinate, some inferior medial setae pectinate; article 6 posterior margin sparsely setose, superior

medial setae long, oblique palm defined by 2 stout spines, small spines spaced along palmar margin. *Gnathopod 2*: larger, more robust than gnathopod 1; article 4 posteroventral corner drawn to a sharp point, anteroventral corner smoothly rounded; article 5 compressed, posteroventral corner setose; article 6, superior medial setae paired, inferior medial setae sparse, posterior margin bearing groups of setae, oblique palm defined by a cusp armed with 2 stout spines, palmar margin spinous; dactylus curved, inner margin sparsely setose.

Peraeopod 3: coxa 1.2 times as wide as long; article 4, 1.3 times as long as article 5, 2 small spines on anterior margin, anteroventral corner broad, armed with large spine; article 5 equal to article 6, posterior margin with 2 pairs of small spines, posteroventral corner armed with 2 large and 1 small spine; article 6, pairs of spines spaced along posterior margin; dactylus apically constricted, inner margin bearing seta and setule at constriction. *Peraeopod 4* very similar in size and proportions to peraeopod 3. *Peraeopod 6*: coxa 1.6 times as wide as long, ventral margin armed with two stout spines; article 2 posterior margin serrate, posteroventral corner acute, anterior margin spinous; articles 4, 5 and 6 subequal; articles 5 and 6, groups of spines spaced along anterior and posterior margins. *Peraeopod 7* very similar in size and proportions to peraeopod 6 except coxa twice as wide as long, ventral margin armed with one stout spine.

Pleonites: posterior margin of dorsal surface of pleonites 1, 2, 3 armed with 21, 29, 26 teeth respectively. *Epimeron 1* with lateral ridge, 2 notches on ventral margin, posterior margin with 4 teeth. *Epimeron 2* with lateral ridge, tooth at posteroventral corner, posterior margin with 5 teeth. *Epimeron 3* ventral margin entire, bearing 3 spines, posterior margin with 12 teeth.

Urosomites 1 and 2: posterior margin of dorsal surface with 18 and 8 teeth respectively. *Urosomite 3*: posterior margin entire. *Uropod 3*: peduncle 0.6 times as long as rami, distal margin spinous; rami equal; outer ramus, distal margin bearing long spines; inner ramus distal and inner margins armed with long spines. *Telson* tumid, wider than long, cleft midway to base, apices each bearing 2 spines and plumose seta, margins of lobes lined with 'stubble-like' spines.

Female not known.

Remarks. The specific epithet *oxyodus* is taken from the Greek for "sharp-toothed", referring to the armature of the pleonites and urosomites of this species.

Ceradocus oxyodus is assigned to the subgenus *Denticeradocus* because pleonites 1-3 are multidentate dorsally. The armature of pleonites 1-3 of *C. oxyodus* is similar to that of *C. serratus* as shown by J.L. Barnard (1972a) but urosomite 1 of *C. serratus* has the dorsal teeth arranged coronately. *Ceradocus oxyodus* is also similar to *C. serratus* in the shortened gland cone of antenna 2, the long article 3 of the mandibular palp, the presence of a strong sharp tooth on epimeron 2, and the even distribution of teeth on urosomites 1 and 2.

J.L. Barnard (1972a) distinguished *C. dooliba* from *C. serratus* on the basis of these characters and he considered that *C. serratus* and *C. dooliba* may be "cryptic or sibling partners". *Ceradocus oxyodus* resembles *C. dooliba* in the normal peduncle of antenna 2 (not shortened as in *C. serratus*) and the palm of gnathopod 2 which is oblique, spinous and defined by a spinous cusp.

Ceradocus oxyodus was found under stones on a sandy beach at low tide.

Distribution. Lizard Island (type locality).

Ceradocus (Ceradocus) woorree n.sp.

Figs 5, 6

Type material. HOLOTYPE, male, 6.9 mm, AM P31714, eastern end of Mangrove Beach, Lizard Island (14°41'S, 145°27.5'E), from sediment, 1.5 m depth, A.R. Jones, 10 October 1978, LI-37; PARATYPE, male, 5.9 mm, AM P31715, Casuarina Beach, Lizard Island (14°40.5'S, 145°26.6'E), under stones at low tide mark, J.K. Lowry, A.R. Jones and P.C. Terrill, 11 October 1978, LI-39.

Diagnosis. Accessory flagellum 5-articulate; coxa 1 anteroventral corner smoothly rounded; second gnathopods asymmetrical, right or left may be larger; palm of larger second gnathopod undefined, spinous with spinous distal protusion; article 2 of peraeopods 5-7, posteroventral corner smoothly rounded; pleonites and urosomites lacking dorsal teeth; posterior and ventral margins of epimera entire; telson longer than wide, deeply cleft, apices tapering to a point, each bearing large spine, 2 small spines, plumose seta.

Description. Holotype male, 6.9 mm. *Head* as long as first two peraeonites, eye brown in alcohol, cheek notch narrow, anteroventral corner obtuse; *Antenna 1*: 1.3 times as long as antenna 2; peduncle and flagellum subequal, article 1 armed with 3 ventral spines, equal to article 2; article 3, 0.3 times as long as articles 1 and 2; flagellum 17-articulate; accessory flagellum 5-articulate, article 5 small, extending to distal margin of article 5 of primary flagellum. *Antenna 2*: peduncle 3 times as long as flagellum, gland cone extending beyond article 3; flagellum 11-articulate.

Mandible with incisor and 7 accessory blades; lacinia mobilis bearing 4 teeth; molar triturating with ragged seta; palp 3-articulate, article 2 twice as long as article 1, article 1 with acute distal process, articles 2 and 3 sparsely setose. *Maxilla 1*: inner plate quadrate with terminal plumose setae; outer plate with fine setae along inner margin, armed with 7 barbed spine teeth; palp 2-articulate, terminally setose. *Maxilla 2*: inner plate ovate, apically setose, line of medial setae, outer plate quadrate, apically setose. *Maxillipeds*: inner plate apex truncate bearing plumose setae, inner marginal setae fine; outer plate ovate, apical setae plumose; palp 4-articulate, article 2 longest, inner margin setose.

Gnathopod 1: coxa quadrate, ventral margin sparsely setose, anteroventral corner smoothly rounded, posteroventral corner notched; article 4 anterior and

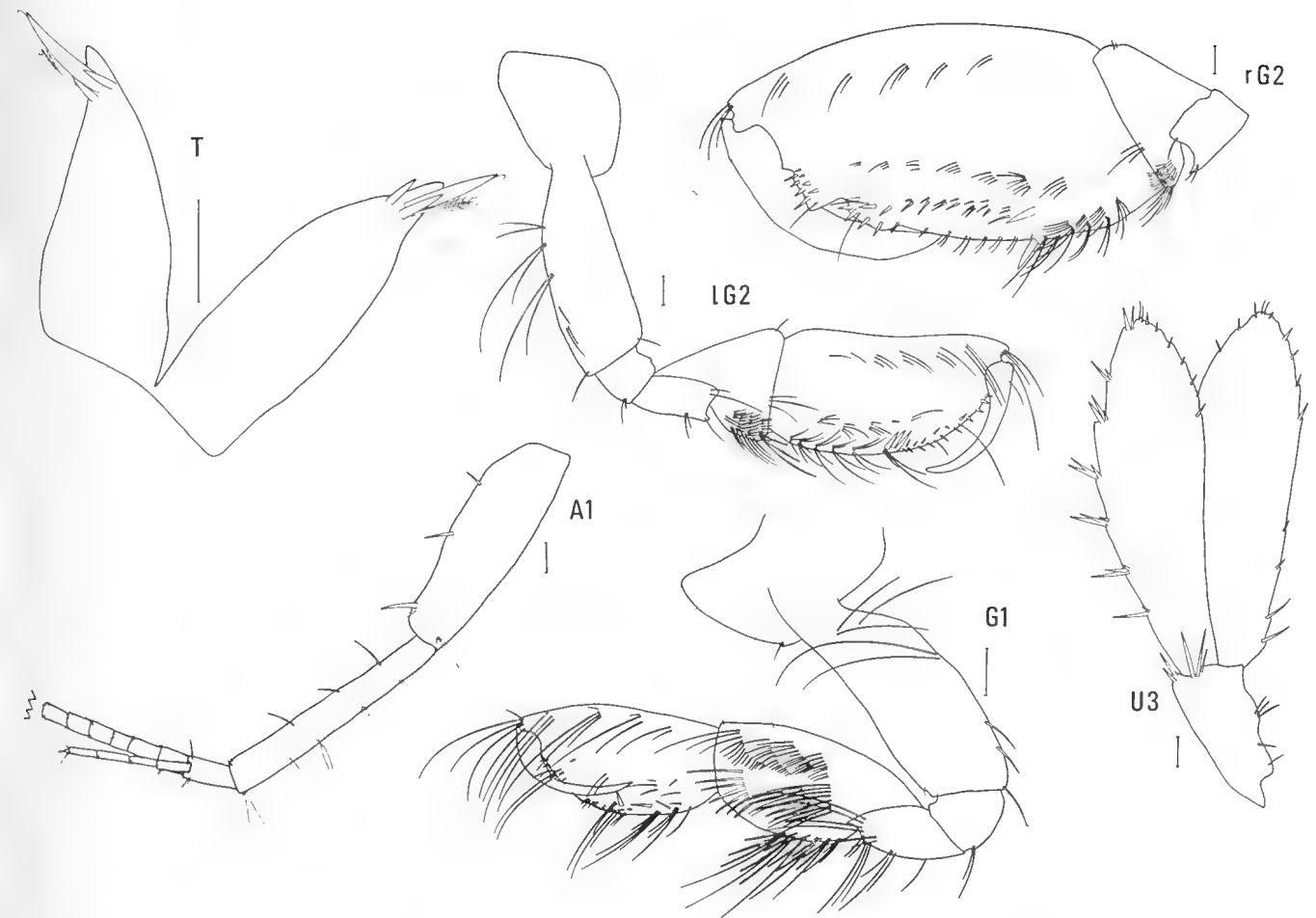


Fig. 5. *Ceradocus woorree* n.sp., holotype, male 6.9 mm, LI-37; gnathopod 1, paratype, male, 5.9 mm, LI-39. Scale lines represent 0.1 mm.

posterior margins converging to acute point, distal setae extending across article 5; article 5 ovate, posterior margin setose with some pectinate setae, 4 rows of superior medial setae, 3 rows of inferior medial setae, the 2 distal rows comprising pectinate setae; article 6 ovate; 0.9 times as long as article 5, posterior margin bearing groups of setae, spines medial to margin, superior medial setae long, oblique palm confluent with posterior margin, defined by stout spine, palm bearing small spines; dactylus slender. *Left gnathopod 2* slightly larger, more robust than gnathopod 1; article 4 posteroventral corner acute; article 5 compressed, posteroventral corner setose; article 6, superior and inferior medial setae short, posterior margin bearing groups of setae, oblique palm confluent with posterior margin defined by 3 stout spines, palm armed with small spines; dactylus slender. *Right gnathopod 2* larger, more robust than gnathopod 1 and left gnathopod 2; article 4 posteroventral corner acute; article 5 compressed, posteroventral corner setose; article 6 robust, 0.6 times as wide as long, 5 groups of short superior medial setae, 7 groups of short inferior medial setae, posterior margin bearing groups of setae, 2 stout spines midway along posterior margin, groups of short setae form line medial to posterior margin, undefined palm confluent with

posterior margin; palm spinous with spinous distal protrusion; dactylus stout.

Peraeopod 3: coxa almost as wide as long; article 4 slightly longer than article 5, setae spaced along anterior margin, broad anteroventral corner bearing seta; article 5, posterior margin sparsely setose; article 6 subequal to article 5, pairs of spines spaced along posterior margin; dactylus apically constricted, inner margin bearing seta and 2 setules at constriction. *Peraeopod 4* very similar in size and proportions to peraeopod 3 except article 4 is 1.3 times as long as article 5. *Peraeopod 5*: coxa 1.3 times as wide as long; article 2, posterior margin entire, longer than anterior margin, posteroventral corner smoothly rounded; article 4 subequal to article 5, ventral margin twice as wide as dorsal margin, anteroventral and posteroventral corners broad; article 5, subequal to article 6; articles 5 and 6, groups of spines spaced along anterior and posterior margins. *Peraeopod 6* very similar in proportions to peraeopod 5 except in following ways: 1.4 times as long as peraeopod 5, coxa 1.5 times as wide as long, article 2 posterior margin slightly serrate, articles 5 and 6 more spinous. *Peraeopod 7* very similar in proportions to peraeopod 5 except in following ways: 1.2 times as long as peraeopod 5, coxa 1.6 times as wide as long, article

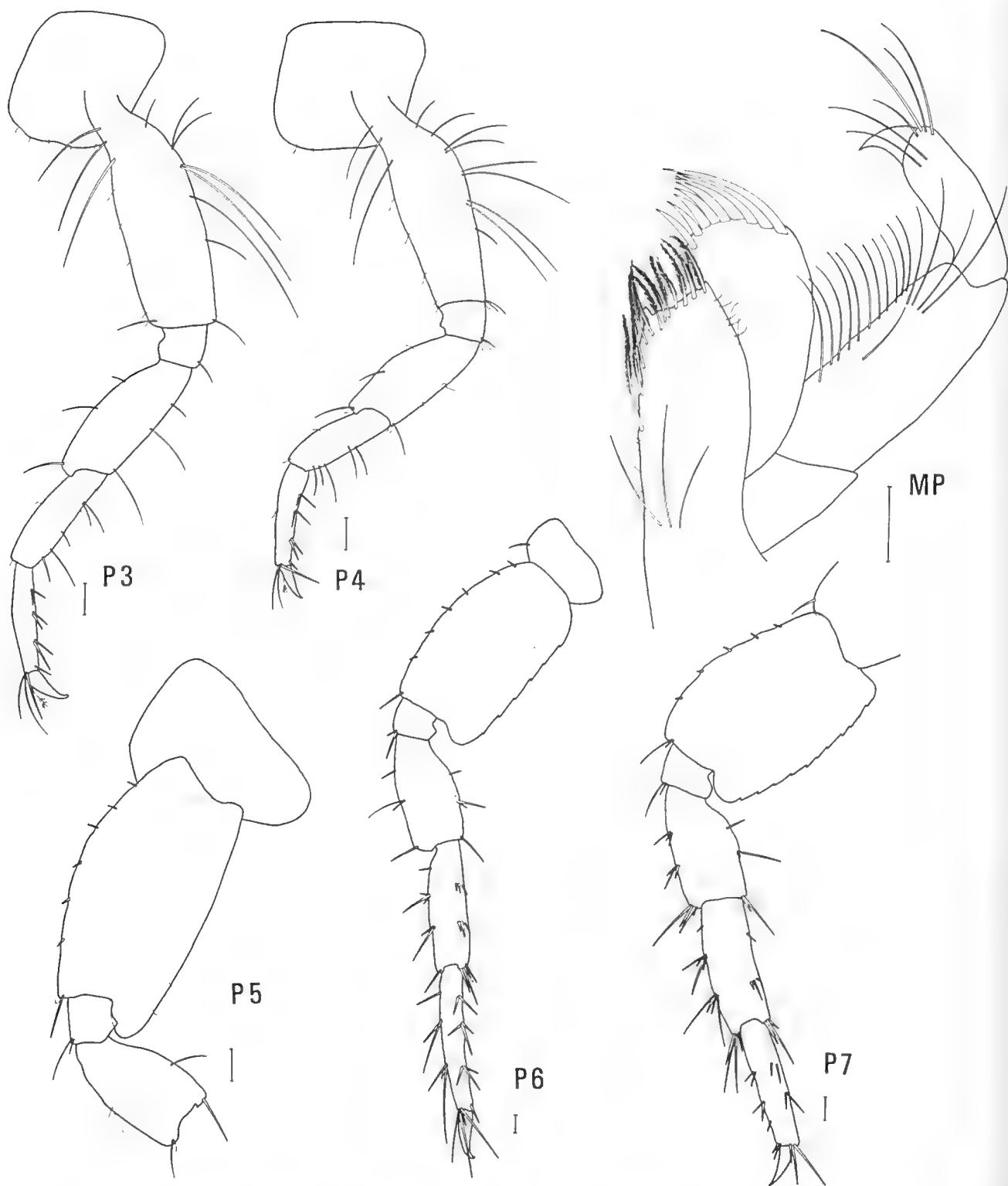


Fig. 6. *Ceradocus woorree* n.sp., holotype, male 6.9 mm, LI-37. Scale lines represent 0.1 mm.

2 posterior margin serrate, articles 4, 5 and 6 more spinous.

Epimera 1, 2, 3 posterior and ventral margins entire, posteroventral corners acute.

Uropod 3: peduncle 0.5 times as long as rami, distal margin spinous; rami equal; outer ramus distal margin bearing small spines, outer margin spinous; inner ramus

distal margin bearing small spines, inner margin sparsely spinous. *Telson* longer than wide, deeply cleft, apices tapering to a point, each bearing large spine, 2 small spines, plumose seta.

Female not known.

Variation. The paratype has the left second gnathopod larger than the right and of the same form

as the right gnathopod of the holotype. Conversely the small right second gnathopod of the paratype is of the same form as the left second gnathopod of the holotype.

Remarks. The specific epithet *woorree* is taken from an Aboriginal word meaning "sea".

Ceradocus woorree is assigned to the subgenus *Ceradocus* because pleonites 1-3 are not multidentate dorsally (Sheard, 1939). *Ceradocus (Ceradocus) woorree* is the only species in the subgenus that lacks dorsal teeth on the urosomites as well as the pleonites. J.L. Barnard (1952) described *C. paucidentatus* from California, which also lacks dorsal teeth on pleonites 1-3 but has 1 or 2 dorsal teeth on urosomite 1, and 1 dorsal tooth on urosomite 2. Fox (1973) considered that *C. paucidentatus* "casts some doubt on the validity of Sheard's (1939) separation" because it lacks a single mid-dorsal tooth on any pleonites and this is a characteristic feature of the subgenus *Ceradocus*. For the same reason *C. woorree* and *C. shoemakeri* Fox, 1973 do not conform with Sheard's (1939) separation.

Ceradocus woorree seems closely related to *C. aviceps* described by K.H. Barnard (1940) from South Africa.

Both these species have telson cleft to base, and posterior and ventral margins of the third pleonal epimeron entire. The gnathopods of *C. aviceps* are distinct from *C. woorree* in that gnathopod 1 has article 5, 3.5 times as long as article 6, and the second gnathopods are symmetrical with a short, stout, strongly hooked dactylus.

Ceradocus woorree was found in sediment and under stones from low tide mark to 1.5 metres depth.

Distribution. Lizard Island (type locality).

Ceradocus (Denticeradocus) yandala n.sp.

Figs 7, 8

Type material. HOLOTYPE, male, 4.5 mm, AM P31718, fringing reef, between Bird Islet and South Island, Lizard Island (14°42'S, 145°28'E), from reef rock, 12 m depth, P.B. Berents and P.A. Hutchings, 11 January 1977, 76 LIZ A; ALLOTYPE, 4.0 mm, AM P31719, type locality, P.B. Berents, 24 August 1976; 3 PARATYPES, AM P31720, type locality, P.B. Berents and P.A. Hutchings, 11 January 1977; 1 PARATYPE, AM P31721, fringing reef, between Bird Islet and

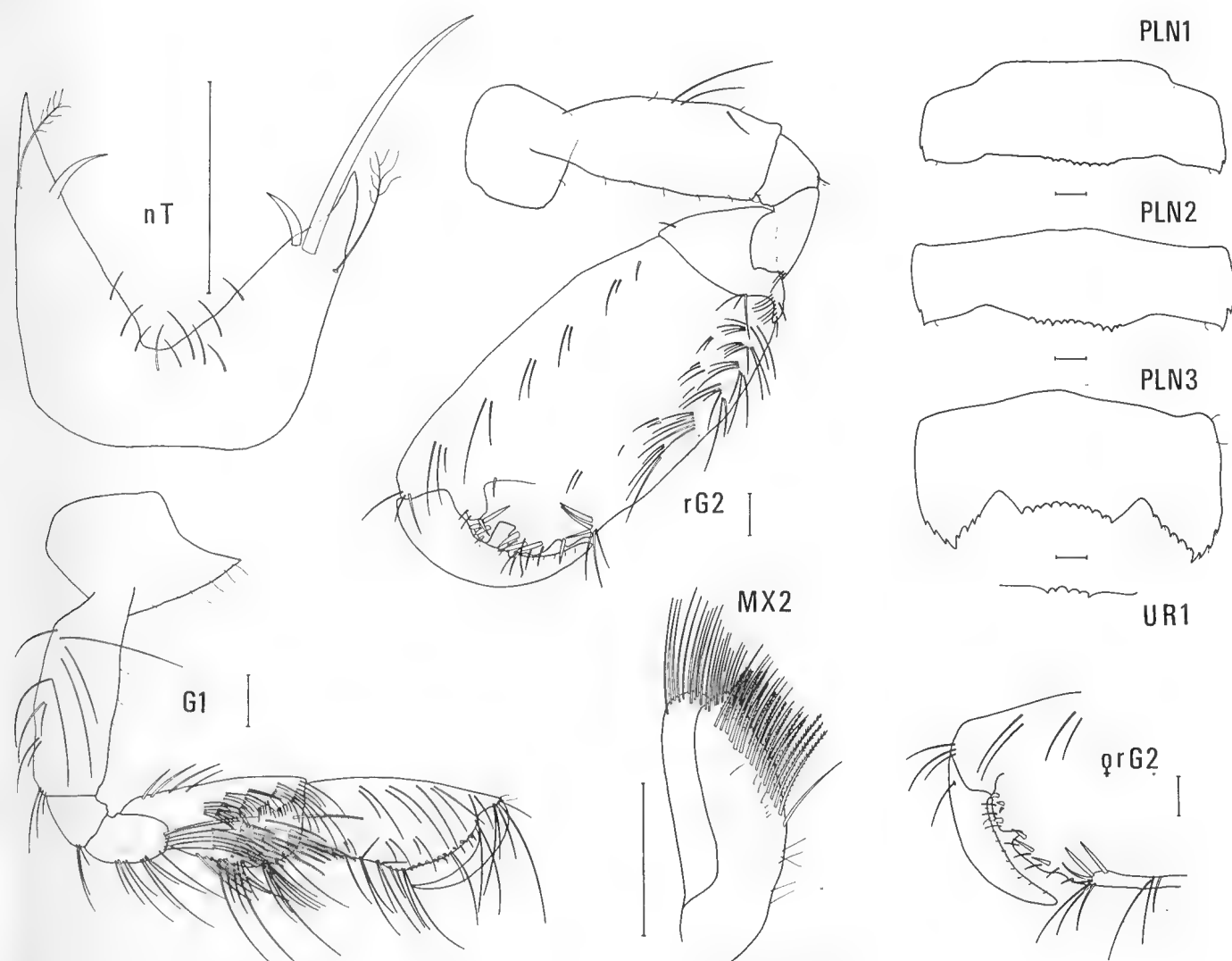


Fig. 7. *Ceradocus yandala* n.sp., holotype, male 4.5 mm, 75 LIZ A; female, allotype, 4.0 mm, 76 LIZ A; n = female, 4.4 mm, 76 LIZ A. Scale lines represent 0.1 mm.

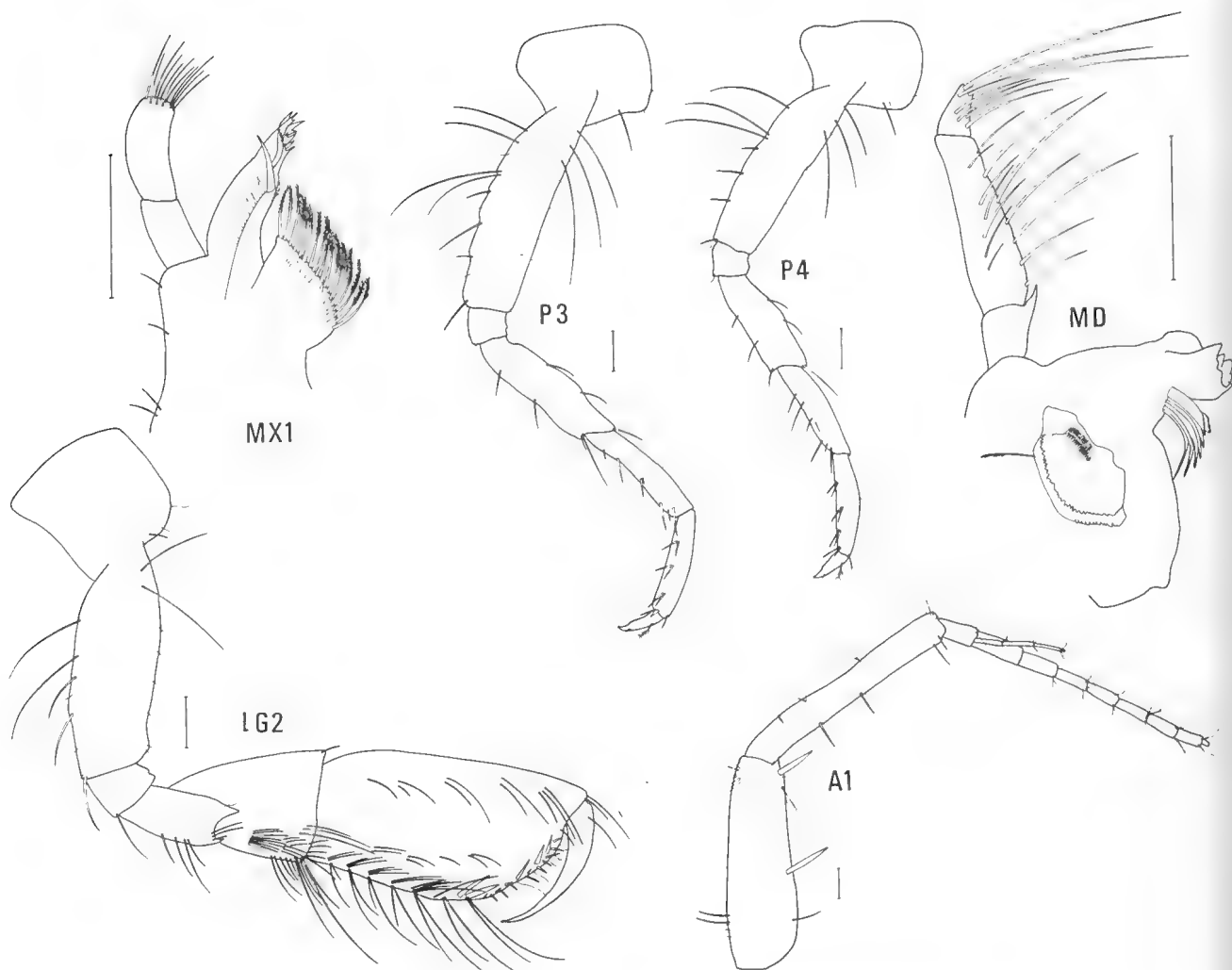


Fig. 8. *Ceradocus yandala* n.sp., holotype, male 4.5 mm, 76 LIZ A. Scale lines represent 0.1 mm.

South Island, Lizard Island ($14^{\circ}42'S$, $145^{\circ}28'E$), from mixed algae and coral rubble, 24–27 m depth, J.K. Lowry, 7 October 1978, LI-21.

Diagnosis. Accessory flagellum 4-articulate; coxa 1 anteroventral corner acute; second gnathopods asymmetrical, article 6 of larger second gnathopod with oblique palm defined by 3 spines, mid-palmar sinus quadrate, palm with proximal indentation armed with spine; posterior margin on pleonites 1, 2, 3 with 9–14, 11–17, 11–18 dorsal teeth respectively; epimera 1 and 2 posterior margin entire; epimeron 3 posteroventral corner acute, posterior and ventral margins serrate; posterior margin of urosomite 1 with 5–7 dorsal teeth; telson as wide as long, cleft 75%, apices tapering to a point, one large and one small spine on each lobe.

Description. Holotype male, 4.5 mm. *Head* slightly longer than first two pereonites; eye dark brown in alcohol, ommatidia discrete; cheek notch gaping, anteroventral corner drawn to sharp point. *Antenna 1*: 1.3 times as long as antenna 2; peduncle longer than flagellum, articles 1 and 2 with 2 ventral spines, article 1 anteroventral corner extended to form sharp cusp,

article 2 longest; flagellum 8-articulate, article 8 small; accessory flagellum 4-articulate, article 4 small, extending beyond article 2 of primary flagellum. *Antenna 2*: peduncle twice as long as flagellum, article 4 longest, article 5 subequal to article 4, cone gland on article 2 extending to M63 on article 3; flagellum 5-articulate.

Mandible with incisor and 7 accessory blades; lacinia mobilis stout; molar triturating with ragged seta; palp 3-articulate, article 3 subequal to article 1, article 2, 2.5 times as long as article 1, article 1 with medial cusp. *Maxilla 1*: inner plate quadrate with 18 terminal plumose setae; outer plate armed with 8 spine teeth; palp 2-articulate, terminally setose. *Maxilla 2*: outer plate with distal setae; inner plate with distal setae and lateral setae on inner margin, stout plumose setae arise medially. *Maxillipeds*: inner plate apex truncate, bearing plumose setae, inner marginal setae long; outer plate ovate, apical setae plumose; palp 4-articulate, article 2 longest, 2.4 times as long as article 1 and dactylus, 1.6 times as long as article 3.

Gnathopod 1: coxa as long as wide, anteroventral corner acute, posteroventral corner notched, ventral

margin sparsely setose; article 5 equal to article 6, 9 rows of medial setae, with some pectinate setae, anterior margin sparsely setose, posterior margin setose with pectinate setae and long simple setae; article 6 with sparse superior medial setae, posterior margin sparsely setose, oblique palm confluent with posterior margin, palmar margin armed with small spines; dactylus slender. *Left gnathopod 2* larger, more robust than gnathopod 1; coxa quadrate; article 4 anteroventral and posteroventral corners sharply produced; article 5, 0.6 times as long as article 6, posteroventral corner setose; article 6, 0.5 times as wide as long, superior and inferior medial setae sparse, oblique palm defined by 2 spines and 3 setae, palmar margin spinous; dactylus slender. *Right gnathopod 2* larger, more robust than gnathopod 1 and left gnathopod 2; coxa quadrate; article 2, 0.4 times as wide as long, anterior and posterior margins sparsely setose, stout medial seta at M 74; article 4 posteroventral corner sharp; article 5 compressed, 0.3 times as long as article 6, posteroventral corner extending along posterior margin of article 6; article 6, 0.6 times as wide as long, superior medial and inferior medial setae sparse, oblique palm defined by 3 spines and 4 setae, mid-palmar sinus quadrate with group of 5 proximal and 3 distal spines, proximal indentation of palm with spine; medial ridge distally; dactylus robust, inner margin sparsely setose.

Peraeopod 3: coxa 1.4 times as wide as long; article 4, 1.2 times as long as article 5; article 5 setae spaced along anterior and posterior margins; article 5, 3 spines along posterior margin, posteroventral corner with 3 spines; article 6 subequal to article 5, 4 pairs of spines including pair of locking spines along posterior margin; dactylus apically constricted, 2 setae and plumose setule at constriction. *Peraeopod 4* very similar in size and proportions to *peraeopod 3*.

Pleonites: posterior margin of dorsal surface of pleonites 1, 2, 3 armed with 10, 13, 11 teeth respectively. *Epimera 1 and 2*: posteroventral corner acute, ventral margin notched. *Epimeron 3*: posteroventral corner defined by sharp tooth, ventral margin bearing 3 teeth, posterior margin serrate with 4 or 5 teeth.

Urosomite 1: posterior margin of dorsal surface bearing 5 teeth. *Telson* as wide as long, cleft 75%, apices tapering to a point, one large and one small spine on each lobe at M70, large spine as long as telson, plumose seta on each lobe proximal to spines, fine setules in cleft.

Allotype female, 4.0 mm. Similar to holotype except in following ways: *Antenna 1*: flagellum longer than peduncle, 16-articulate, article 16 small; accessory flagellum extending beyond article 3 of primary flagellum.

Maxilla 1: inner plate bearing 13 terminal seta.

Gnathopod 1: palmar margin less spinous. *Right gnathopod 2*: palmar margin less spinous, sinus and indentation of palm smaller. *Peraeopods 3 and 4*: articles 5 and 6 less spinous. *Pleonites*: posterior margin of dorsal surface of pleonites 1, 2, 3 armed with 9, 11, 14 teeth respectively. *Epimeron 3*: ventral margin bearing 2 teeth.

Variation. Inner plate of maxilla 1 may have 13–18 terminal plumose setae. A 4.4 mm female was found with the outer plate of maxilla 1 bearing 9 spine teeth. All material examined exhibited asymmetry of gnathopod 2, and either the right or left gnathopod may be enlarged.

Remarks. The specific epithet *yandala* is taken from an Aboriginal word meaning “spear with a long point”, which alludes to the shape of the third epimeron.

Ceradocus yandala is assigned to the subgenus *Denticeradocus* because pleonites 1–3 are multidentate dorsally. *Ceradocus yandala* resembles *C. mahafalensis*, which Ledoyer (1979) described from Madagascar. The armature of pleonites 1–3 and urosomite 1 is similar but urosomite 2 is toothed in *C. mahafalensis*. The palm of the larger second gnathopod of *C. mahafalensis* is less spinous and does not have a quadrate mid-palmar sinus. Both species have the gland cone of antenna 2 extending about $\frac{2}{3}$ along article 3 of the peduncle but the telson in *C. mahafalensis* is longer than wide and the apices more spinous than in *C. yandala*.

Ceradocus yandala was found in algae, coral rubble and reef rock samples taken around Lizard Island to depths of 27 metres.

Distribution. Lizard Island (type locality).

Genus *Dulichchiella* Stout

Karaman and Barnard (1979) revived the genus *Dulichchiella* Stout for those species within the genus *Melita* that have male gnathopod 2 showing strong diversity from right to left sides. The species included in *Dulichchiella* were *D. appendiculata* (Say), *D. australis* (Haswell), *D. exilii* (Fritz Müller), *D. fresneli* (Audouin) and *D. spinosa* (Stout).

Two species of *Dulichchiella* have previously been recorded in Australia. *Dulichchiella australis* (Haswell, 1880a) was described from Port Jackson. *Dulichchiella fresneli* has been recorded by Stebbing (1910) from off Manning River and Botany Bay, and by Chilton (1921) from Sanders Bank, Kangaroo Island.

Dulichchiella appendiculata was found in the material from Lizard Island and adjacent reefs.

Dulichchiella appendiculata (Say, 1818)

Fig. 9

Gammarus appendiculatus Say, 1818:377–379.

Melita appendiculata.—Stebbing, 1906:428; J.L. Barnard, 1962: 107, 109; 1970:161, fig. 101; 1971:85; Feeley and Wass, 1971:17; Griffiths, 1973:286; 1974a: 191; 1974b:237; Ledoyer, 1978:282; 1979:86, fig. 50; Ortiz, 1978:8; Hirayama and Kikuchi, 1979:67–77, figs 2–6.

Dulichchiella appendiculata.—Karaman and Barnard, 1979:152–153.

Material. AM P30123 to AM P30126 from the following stations: 75 LIZ D-1 (1), L1-2 (6), L1-27 (5), L1-28 (2).

Diagnosis. Accessory flagellum 4–5 articles; male second gnathopods asymmetrical, article 6 and dactylus

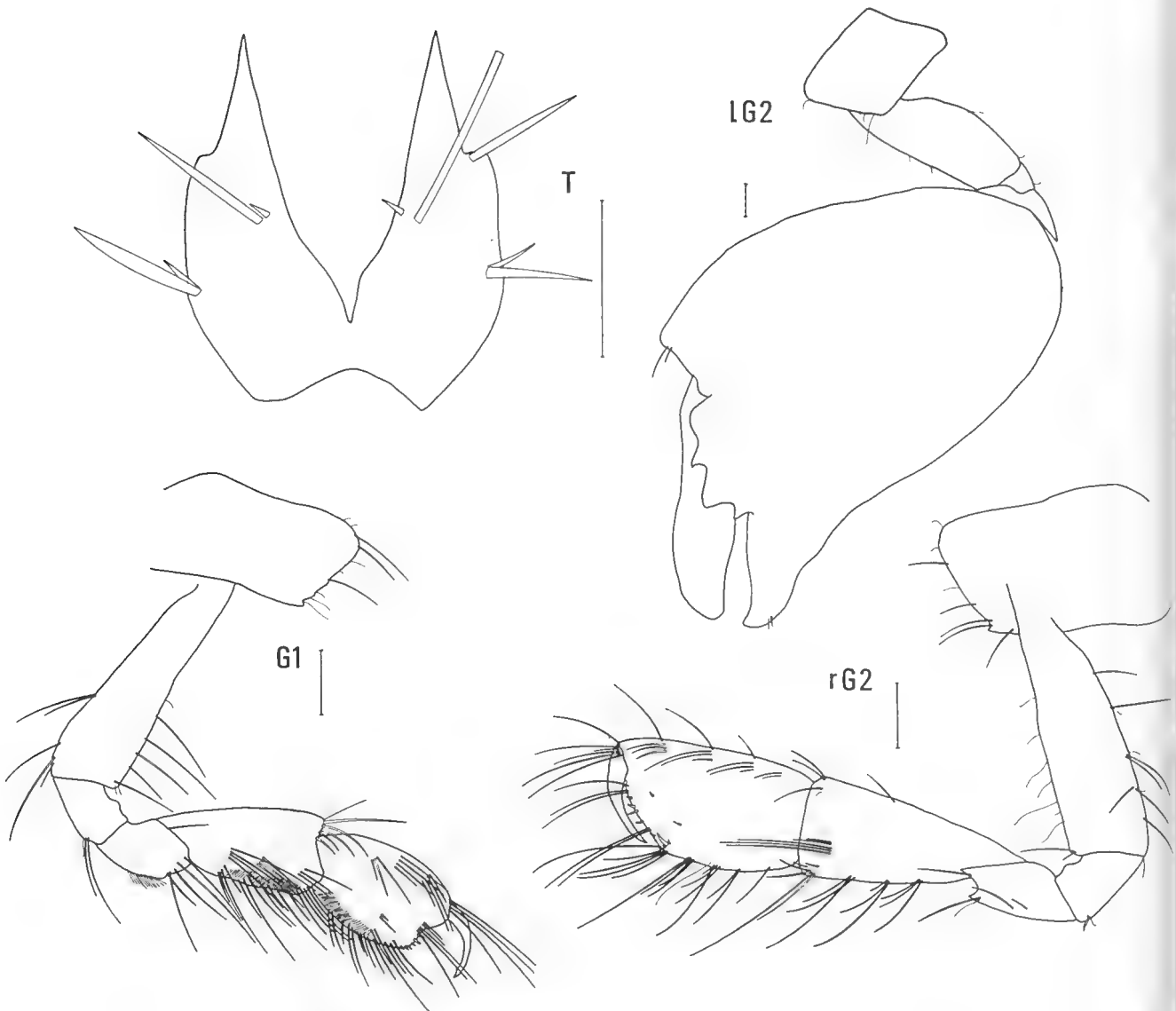


Fig. 9. *Dulichiella appendiculata* (Say), male, 4.3 mm, LI-28. Scale lines represent 0.1 mm.

of larger second gnathopod much enlarged; dactylus of peraeopods with accessory tooth; pleonites 1-3 with 7 dorsal teeth on posterior margin; third pleonal epimeron with posteroventral corner extended to sharp cusp; telson longer than wide, deeply cleft.

Remarks. *Dulichiella appendiculata* was described from Georgia, U.S.A. (Say, 1818). It has been reported from Hawaii, Chesapeake Bay, east and west coasts of southern Africa, Mauritius, Cuba, Madagascar and Japan. Feeley and Wass (1971) recorded *D. appendiculata* from the York River in Chesapeake Bay from waters of 13.6‰ salinity. It seems unlikely that the same species occurs on the Great Barrier Reef and in estuarine conditions on the east coast of the United States.

Dulichiella fresneli (Audouin) was described from Egypt and has also been reported with an extensive geographical distribution. *Dulichiella appendiculata* and *D. fresneli* were synonymized by J.L. Barnard (1970)

as *D. appendiculata*, but Karaman and Barnard (1979) revived *D. fresneli*. Many records of these species do not give descriptive details of figures.

Say's (1818) original description was not detailed but he did note that pleonites 1-3 had seven dorsal teeth on the posterior margins. The material examined from Lizard Island has seven dorsal teeth in a consistent pattern on pleonites 1-3. J.L. Barnard's (1970) material from Hawaii also had seven dorsal teeth in the same pattern as the Lizard Island material. J.L. Barnard (1962) noted a dorsal tooth formula of 7-7-7 for pleonites 1-3 but did not illustrate the pattern of armature.

The material from Lizard Island closely resembles J.L. Barnard's (1970) Hawaiian material and must be assigned to *Dulichiella appendiculata* since it fits Say's (1818) description.

Dulichiella appendiculata was found in reef rock covered in coralline algae *Halimeda* and *Lithothamnion*

at Yonge Reef, at a depth of 36 metres on the outer slope. At Lizard Island it was found in seagrass *Halophila* and algae *Caulerpa*, *Udotea* and drift algae from 7 to 27 metres.

Distribution. Georgia, U.S.A. (type locality); Hawaii; Chesapeake Bay; Mozambique; SW Africa; Natal; Mauritius; Cuba; Madagascar; Japan; Lizard Island; Yonge Reef.

Genus *Elasmopus* Costa

Sheard (1937) listed seven species of *Elasmopus* occurring in Australia; however, five of these have since been transferred to other genera. *Elasmopus boeckii* (Haswell) and *E. viridis* (Haswell) are now in the genus *Maera*; *E. diemenensis* (Haswell) and *E. subcarinatus* (Haswell) are transferred to *Mallacoota*; and *E. suensis* (Haswell) to *Parelmopus*. The Australian species remaining in *Elasmopus* are *E. rapax* (Costa) and *E. crassimanus* (Miers) from Port Jackson. J.L. Barnard (1958) considered the latter to be a dubious species.

J.L. Barnard (1974) recorded three species of *Elasmopus* from southern Australia: *E. yunde* Barnard, *E. menurte* Barnard and *E. bollonsi* Chilton. He found *Elasmopus* to be a rare genus in the collection examined from warm temperate Australia. In the material examined from Lizard Island and adjacent reefs, *Elasmopus* was found to be a diverse and abundant genus which suggests that the genus is more successful in tropical Australia than in temperate Australia.

The number of species of *Elasmopus* recorded in Australia is increased by five with the material from Lizard Island and adjacent reefs.

Elasmopus crenulatus n.sp.

Figs 10, 11, 12

Type material. HOLOTYPE, male, 3.5 mm, AM P30095, off Chinaman's Ridge, Watson's Bay, Lizard Island (14°40'S, 145°27'E), from reef rock, 7 m depth, P.A. Hutchings, 28 July 1977, 76 LIZ B; ALLOTYPE, 4.8 mm, AM P30096, type locality, P.B. Berents, 25 August 1976; 2 PARATYPES, AM

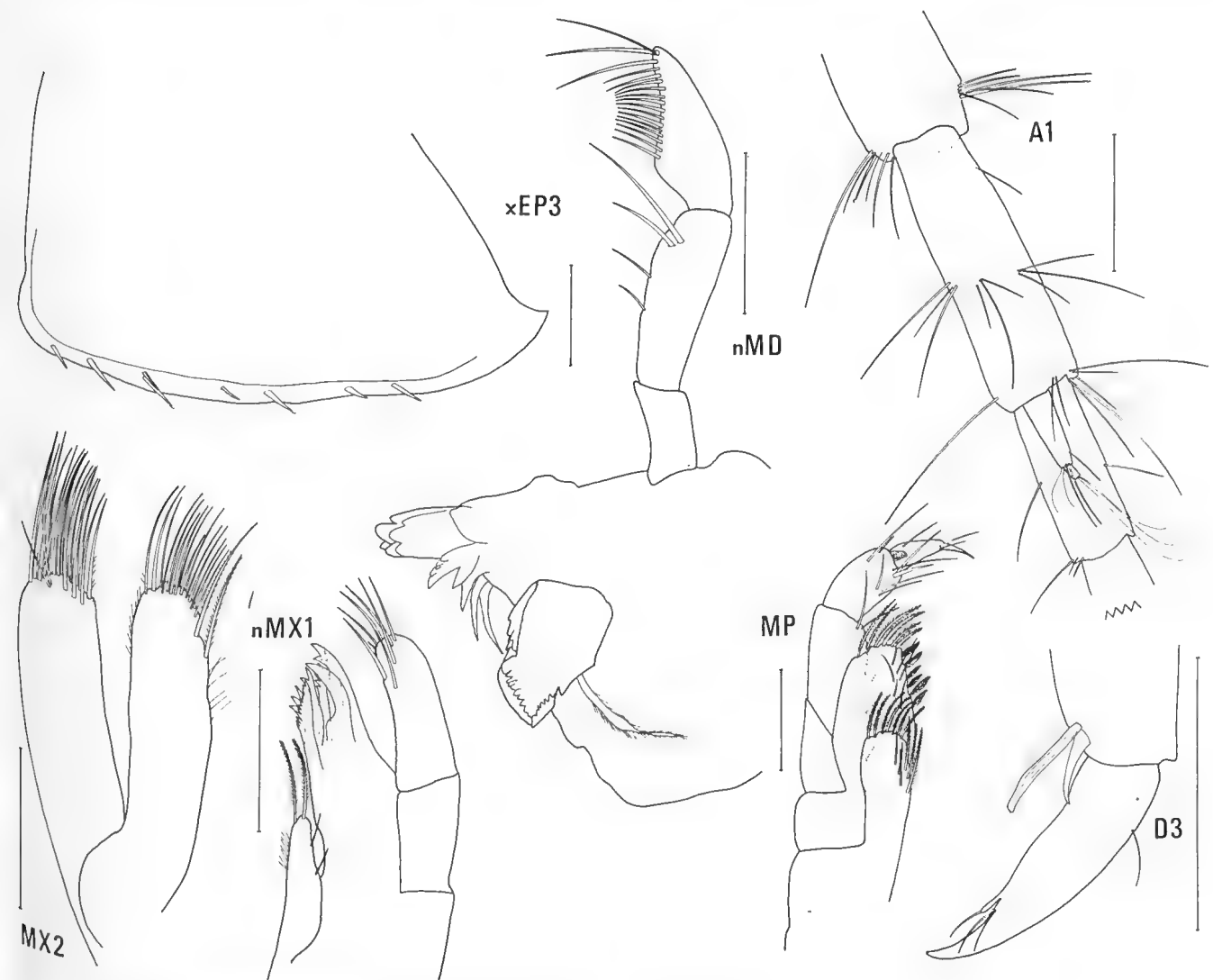


Fig. 10. *Elasmopus crenulatus* n.sp., holotype, male, 3.5 mm, 76 LIZ B; n = male, 3.3 mm, 76 LIZ B; x = male, 2.5 mm, 76 LIZ B. Scale lines represent 0.1 mm.

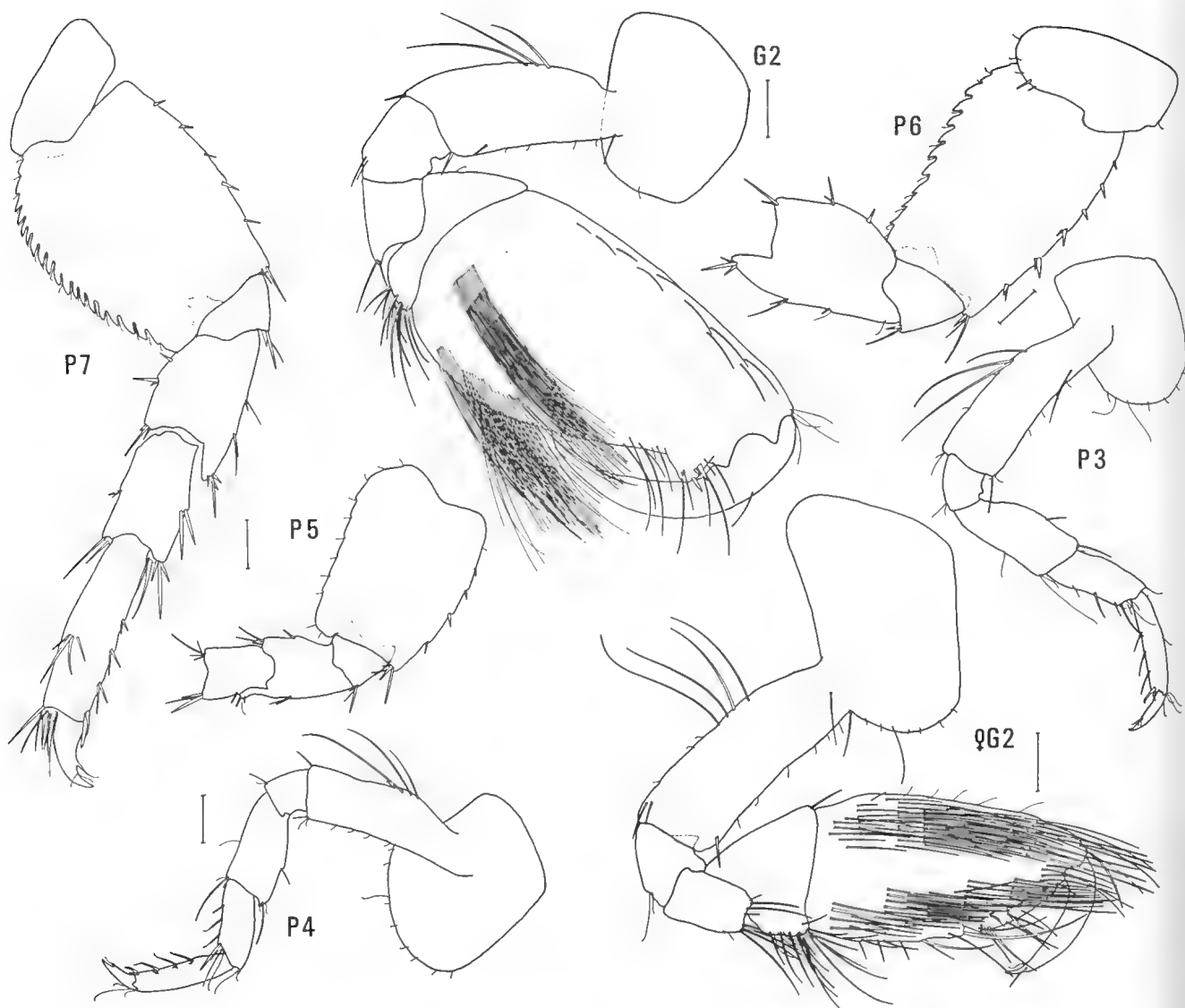


Fig. 11. *Elasmopus crenulatus* n.sp., holotype, male, 3.5 mm, 76 LIZ B; female = allotype, 4.8 mm, 76 LIZ B. Scale lines represent 0.1 mm.

P30097, type locality, P.A. Hutchings, 28 July 1977; 2 PARATYPES, AM P30098, type locality, P.B. Berents and P.M. Berents, 8 April 1977; 2 PARATYPES, male, 3.3 mm, USNM 190703, female, 3.8 mm, USNM 190702, type locality, P.B. Berents and P.A. Hutchings, 19 January 1978; 3 PARATYPES, BMNH 1981:623:3, type locality, male 2.5 mm, P.B. Berents and P.A. Hutchings, 19 January 1978; male, 3.3 mm, P.A. Hutchings, 28 July 1977; female, 3.3 mm, P.B. Berents and P.M. Berents, 8 April 1977.

Additional material. AM P30099 to AM P30105 from the following stations: 75 LIZ 1-2 (1), 76 LIZ A (1), 76 LIZ B (1), LI-1 (8), LI-11 (4), LI-48 (5), LI-50 (4); 3 specimens, AM P31722, between Direction Island and Prison Island, Cocos (Keeling) Islands, Indian Ocean (12°5'S, 96°53'E), from dead coral and encrusting algae in channel in reef crest, 4 m depth, F.H. Talbot, 8 October 1979.

Diagnosis. Accessory flagellum 2-articulate; article 5 of male gnathopod 2 compressed, posterior lobe setose; article 6 of male gnathopod 2 ovate, dense medial setae covering palmar region, palm densely setose with

distal spinous protrusion; article 6 of peraeopods 3 and 4 with distal pair of locking spines comprising large striate chisel spine and smaller unstriate curved spine; article 2 of peraeopods 5-7 lacking long posterior setae; article 2 of peraeopods 6 and 7 crenulate for entire margin; article 6 of peraeopods 5-7 with distal pair of unequal slightly curved striate locking spines; third pleonal epimeron with posteroventral cusp, posterior margin entire; telson as wide as long, cleft midway, inner margin of lobes extended to form apical points, each with 2-3 apical spines.

Description. Holotype male, 3.5 mm. *Head* as long as first two peraeonites; eye dark brown in alcohol, ommatidia discrete, cheek notch narrow. *Antenna 1* almost twice as long as antenna 2; peduncle longer than flagellum, article 1 with distal spine, article 2 subequal to article 1, article 3, 0.6 times as long as article 2; flagellum 8-articulate; accessory flagellum 0.5 times as long as first article of primary flagellum, 2-articulate.

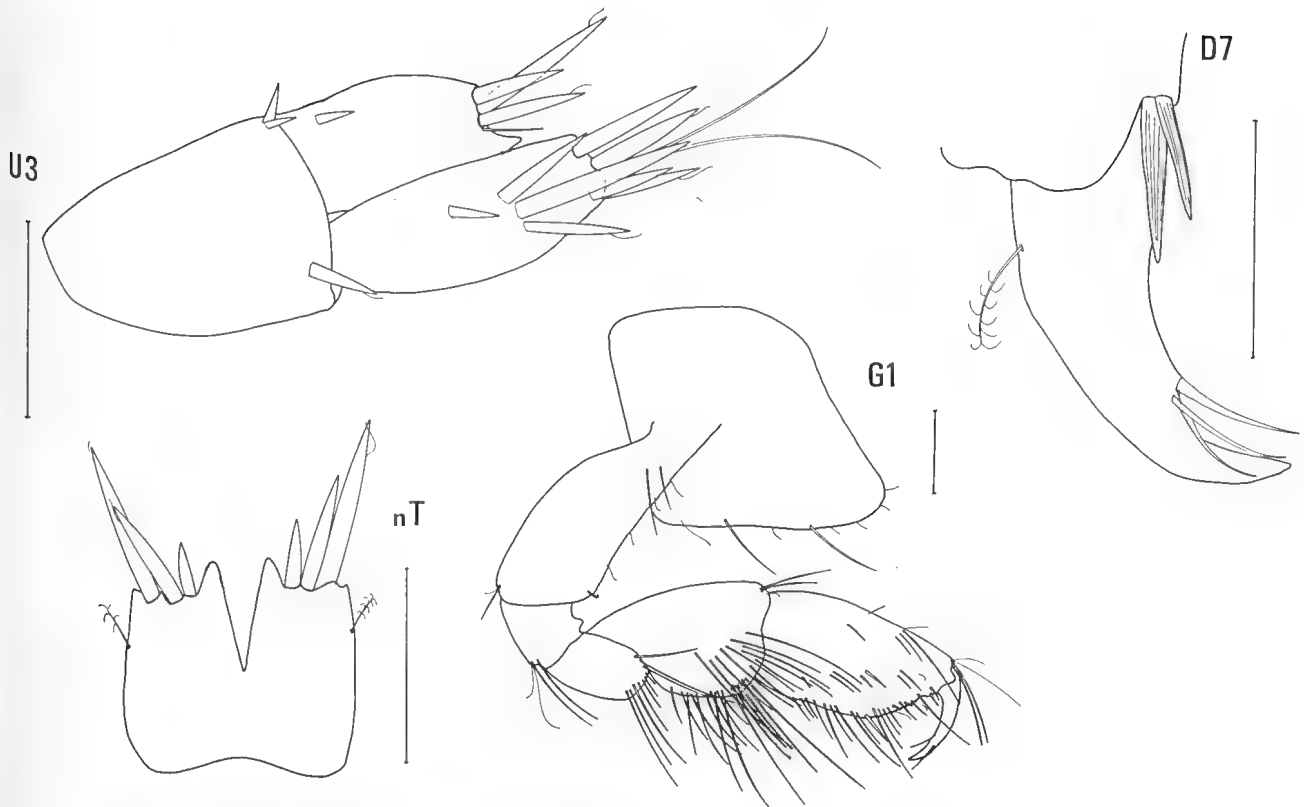


Fig. 12. *Elasmopus crenulatus* n.sp., holotype, male 3.5 mm, 76 LIZ B; n = female, 3.8 mm, 76 LIZ B. Scale lines represent 0.1 mm.

article 2 small. *Antenna 2*: peduncle longer than flagellum, article 3 longest, article 4 subequal to article 3; flagellum 6-articulate.

Mandible with incisor and 3 accessory blades; lacinia mobilis bifid; molar triturating with ragged seta; palp 3-articulate, article 2, 1.7 times as long as article 1, article 3 falcate with comb-like row of medial setae.

Maxilla 1: inner plate with 2 terminal plumose setae and fine marginal setae; outer plate broad, armed with 7 barbed spine teeth; palp 2-articulate, distally setose.

Maxilla 2: inner and outer plate with distal setae, outer plate with fine medial and marginal setae. *Maxillipeds*: inner and outer plates with plumose apical and inner marginal setae; palp 4-articulate, article 2, 1.6 times as long as article 1, articles 3 and dactylus equal and subequal to article 1, pincushion lobe at articulation of article 3 and dactylus.

Gnathopod 1: coxa almost as long as wide, anteroventral corner produced and smoothly rounded, ventral margin sparsely setose; article 5 anterior margin twice as long as posterior margin, posterior margin setose with some pectinate setae, setae arising medially; article 6 twice as long as wide, posterior margin setose, 4 pairs of inferior medial setae, oblique palm defined by stout spine, palm with sparse setae and spines; dactylus bearing 2 setae extending length of palm.

Gnathopod 2 larger, more robust than gnathopod 1; coxa almost as wide as long; article 2, 1.2 times as long as coxa, strong seta on each of anteroventral and

posteroventral corners; article 5 compressed, posterior margin setose; article 6 ovate, posterior margin densely setose, dense medial setae covering palmar regions, oblique palm confluent with posterior margin, densely setose with distal spinous protrusion; dactylus slender.

Peraeopod 3: coxa 1.4 times as long as wide; article 2, 1.3 times as long as coxa; article 5 with setae spaced along posterior margin; article 6 with setae spaced along posterior margin, distal pair of locking spines comprising one striate chisel spine and one unstriate curved spine; dactylus apically constricted, inner margin bearing seta and two setules at constriction. *Peraeopod 4* very similar in size and proportions to peraeopod 3 except: coxa 1.2 times as long as wide, articles 5 and 6 more setose. *Peraeopod 5*: article 2, anterior margin bearing small spines, posterior margin weakly serrate, sparsely setose and lacking long setae, article 4 anterior margin produced halfway along article 5; article 5, 0.6 times as long as article 4. *Peraeopod 6*: coxa 1.8 times as wide as long with 2 posteroventral spines and several setae; article 2 anterior margin spinous, posterior margin crenulate for entire margin, each crenulation with a seta projecting from within; article 4 anterior margin extended downwards. *Peraeopod 7* more robust and setose than peraeopod 6; coxa twice as wide as long; article 2 anterior margin spinous, posterior margin crenulate for entire margin, each crenulation with a seta projecting from within; article 4 anterior margin produced downwards; article 5, 0.8 times as long as

article 4, anterior and posterior margins spinous; article 6, 1.5 times as long as article 5, anterior margin spinous, distal pair of unequal slightly curved striate locking spines; dactylus apically constricted, inner margin with a seta and 2 setules at constriction.

Third pleonal epimeron with posteroventral cusp, ventral margin bearing single spines and one pair of spines, posterior margin entire.

Uropod 3: peduncle equal to outer ramus, distal margin spinous; outer ramus with 3 apical spines and 2 long setae, 3 spines at M66, single spines medially at M12 and M45; inner ramus 0.7 times as long as outer ramus, bearing 3 apical spines and a short seta. *Telson* as wide as long, cleft midway to base, inner margins of lobes extended to form apical points each with 3 apical spines.

Allotype female, 4.8 mm. Similar to holotype except in following ways: *Gnathopod 2*: coxa 0.7 times as wide as long; article 6 elongate, superior and inferior medial setae in rows for length of article, palmar margin partly obscured by inferior medial setae, palm defined by stout spine, sparsely setose with row of submarginal spines; oostegite slender, as long as article 2, with 4 lateral and 1 terminal brood setae. *Telson* with 2 apical spines on 1 lobe, 3 apical spines on other.

Variation. Accessory flagellum varies from half as long as article 1 of primary flagellum, to as long as article 1 of primary flagellum. The outer ramus of uropod 3 may have 3-5 apical spines, and the inner ramus may have 2 or 3 apical spines. The telson may have 2 or 3 apical spines on each lobe. Females smaller than the allotype have article 6 of gnathopod 2 less setose.

Remarks. The specific epithet *crenulatus* (L. *crenula* = a notch) refers to the characteristic posterior margin of the second article of peraeopods 6 and 7.

Elasmopus crenulatus shows some similarities with *E. yunde* Barnard from Western Australia in the densely setose palmar region of the male gnathopod 2 and the crenulate posterior margin of article 2 of peraeopod 7. However, *E. yunde* is only crenulate for the distal half of the posterior margin of article 2 of peraeopod 7 and peraeopod 6 lacks any crenulation of the margin. The telson of both species is similar but that of *E. yunde* is more deeply cleft.

Elasmopus crenulatus also shows similarity to *E. serricatus* Barnard from California, Galapagos Islands, Ecuador and Panama. *Elasmopus serricatus* has a crenulate posterior margin of article 2 of peraeopod 7 but article 2 of peraeopod 6 is not crenulate. The palm of the male second gnathopod of *E. serricatus* is densely setose and has a distal spinous protrusion similar to that of *E. crenulatus*. *Elasmopus serricatus*, however, also has a naked tooth on the mid-palm, and the posterior margin of the third pleonal epimeron is notched. The telson of *E. serricatus* is similar to that of *E. crenulatus*; however, in the male the apical spines are shown by J.L. Barnard (1979) to be subterminal, which is characteristic of the *E. rapax* group. The apical spines of the telson

of *E. crenulatus* are terminal, which suggests that this species does not fit J.L. Barnard's definition of the *E. rapax* group.

The male second gnathopod of *E. pecteniscus* (Bate) is similar to that of *E. crenulatus* but the medial face of article 6 is less setose. Peraeopod 6 of *E. pecteniscus* has an extended lobe on the posteroventral margin of article 2 which is crenulate, but the rest of the margin and the posterior margin of article 2 of peraeopod 7 are not crenulate.

Elasmopus crenulatus was found in algae, including the brown algae *Dictyota* and the green algae *Chlorodesmis*, coral rubble and reef rock samples taken around Lizard Island to depths of 12 metres.

Distribution. Lizard Island (type locality); Cocos (Keeling) Islands.

Elasmopus hooheno Barnard, 1970

Fig. 13

Elasmopus hooheno J.L. Barnard, 1970:120-121, fig. 70.—1971:71, 74-75, figs 33-35; Ledoyer, 1972:217, pls 35, 36; 1978:269-271; 1979:69, fig. 40.

Material. AM P30106 to AM P30110 from the following stations: 76 LIZ A (1), 76 LIZ B (68), 76 LIZ 16 (3), LI-11 (3), LI-48 (1); 5 specimens, AM P31824, between Direction Island and Prison Island, Cocos (Keeling) Islands, Indian Ocean (12°5'S, 96°53'E), from dead coral and encrusting algae in channel in reef crest, 4 m depth, F.H. Talbot, 8 October, 1979.

Diagnosis. Accessory flagellum 2-articulate; article 5 of gnathopod 2 compressed, posterior lobe sparsely setose; article 6 of gnathopod 2 tapering distally, oblique palm confluent with posterior margin, palmar margin defined by cusp, mid-palmar cusp setose, distal protrusion spinous; article 6 of peraeopods 3 and 4 with distal pair of locking spines comprising large striate chisel spine and smaller simple spine; article 6 of peraeopods 5-7 with distal pair of striate simple locking spines; posterior margin of third pleonal epimeron serrate; telson wider than long, lobes weakly excavate apically, each bearing 2-3 spines.

Remarks. J.L. Barnard noted in his description of *E. hooheno* that he probably had not described any terminal males, and the holotype he designated is a male 4.3 mm in length. The material I examined provided the opportunity to study males up to 6.3 mm in length, but it is not known whether these are terminal males. The material examined here differs from Barnard's description in the following ways: *gnathopod 2*: in all males examined the dactylus is shorter than the palm, and articles 5 and 6 may be more setose; *peraeopods 3-4*: distal locking spines on article 6 are not as strongly sabre-shaped but resemble a chisel spine; *peraeopods 5-7*: more setose in larger males. *Third pleonal epimeron* ventral margin is more setose and the posterior margin more serrate in larger males, as predicted by Barnard (1970). *Telson*: larger males have three apical spines.

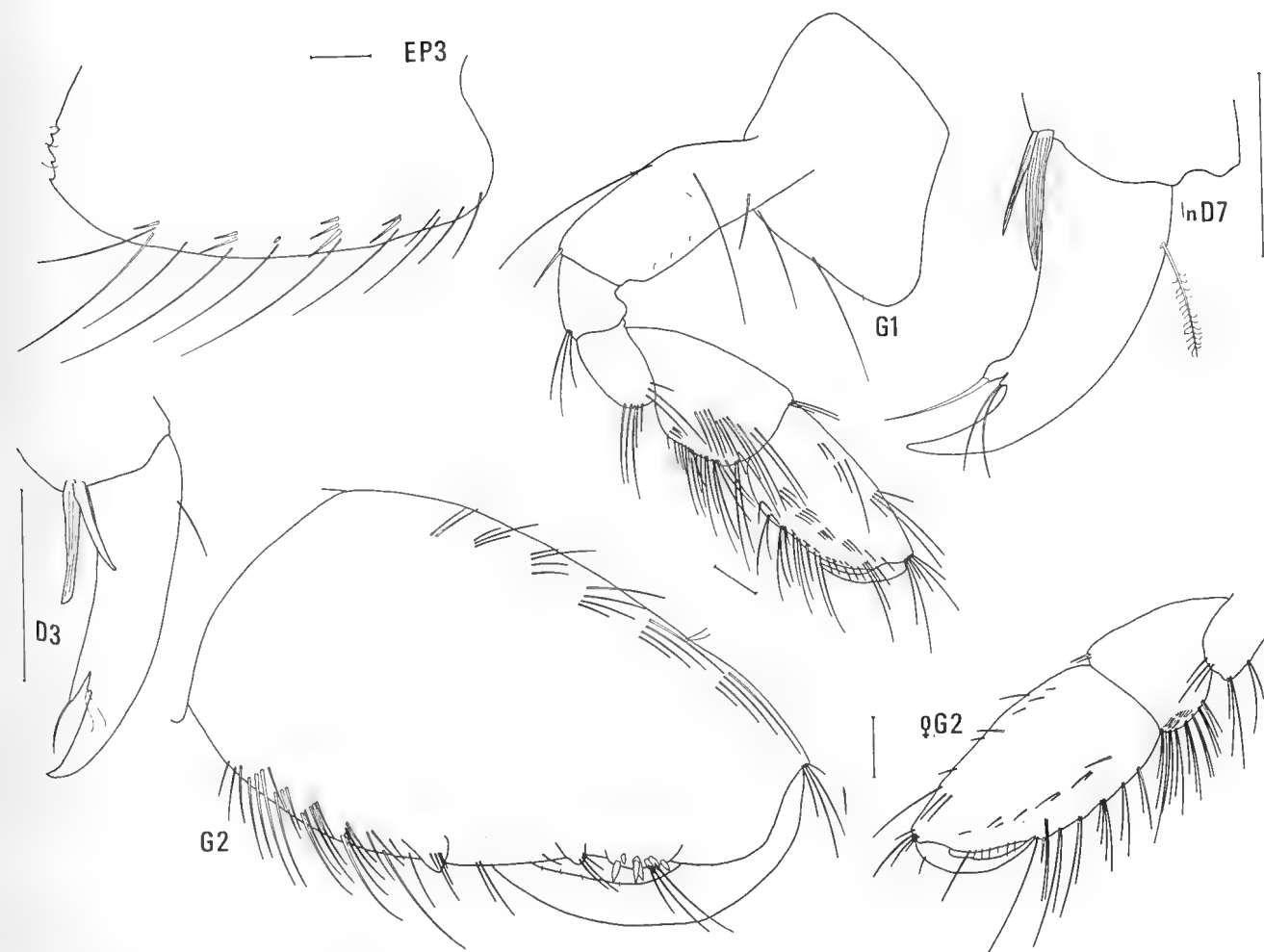


Fig. 13. *Elasmopus hooheho* Barnard, male, 6.3 mm, 76 LIZ B; n = male, 4.2 mm, 76 LIZ B; female, 3.3 mm, 76 LIZ A. Scale lines represent 0.1 mm.

Elasmopus hooheho was found in large numbers in algae, coral rubble and reef rock samples taken in shallow water around Lizard Island.

Distribution. Hawaii (type locality); Madagascar; Mauritius; Lizard Island; Cocos (Keeling) Islands.

Elasmopus pocillimanus (Bate, 1862)

Fig. 14

Moera pocillimanus Bate, 1862:191-192, pl. 34, fig. 7.
Maera pocillimanus.—Stebbing, 1888:35.
Elasmopus pocillimanus.—Della Valle, 1893:733, pl. 1, fig. 4, pl. 22, figs 23-25; Stebbing, 1906:443-444; Chevreux, 1910:225, pl. 16, figs 1, 2; Kunkel, 1910:56-59, fig. 21; Chevreux and Fage, 1925:246-247, fig. 257; Schellenberg, 1938:56, fig. 28; J.L. Barnard, 1970:130-131, figs 77-78; 1971:71, 75, figs 34-35; Ledoyer, 1972:217, 219, pl. 37; 1973:52, 91; 1979:73; Ortiz, 1978:7.
Elasmopus levis.—Kunkel, 1918:103, fig. 24 (*fide* Schellenberg, 1938).

Material. AM P30111 to AM P30113 from the following stations: 75 LIZ T-1 (1), 75 LIZ V-3 (1), 76 LIZ 16 (2).

Diagnosis. Accessory flagellum 1-4 articles; article 5 of gnathopod 2 compressed, posterior lobe setose; article 6 of gnathopod 2 with oblique palm confluent with posterior margin, palmar margin with slight distal spinous protrusion, medial palmar face with hollow defined by ridge bearing 2 spines; article 6 of pereopods 3 and 4 with distal pair of large striate sabre spines; article 6 of pereopods 5-7 with distal pair of striate locking spines comprising one large sabre spine and one simple curved spine; third pleonal epimeron with posteroventral cusp, posterior margin entire; telson as wide as long, cleft 60%, apices rounded, each lobe with one mid-lateral spine and pair of setules.

Remarks. My material is very similar to J.L. Barnard's (1970) Hawaiian material. The anteroventral corner of the head is rounded with an incision as described by Schellenberg (1938) and figured by J.L. Barnard (1970) rather than sharp as figured by Chevreux and Fage (1925). The accessory flagellum of Chevreux and Fage's (1925) material is 2-articulate, that of Schellenberg's (1938) specimen has only one article, and J.L. Barnard (1970) stated that the accessory flagellum

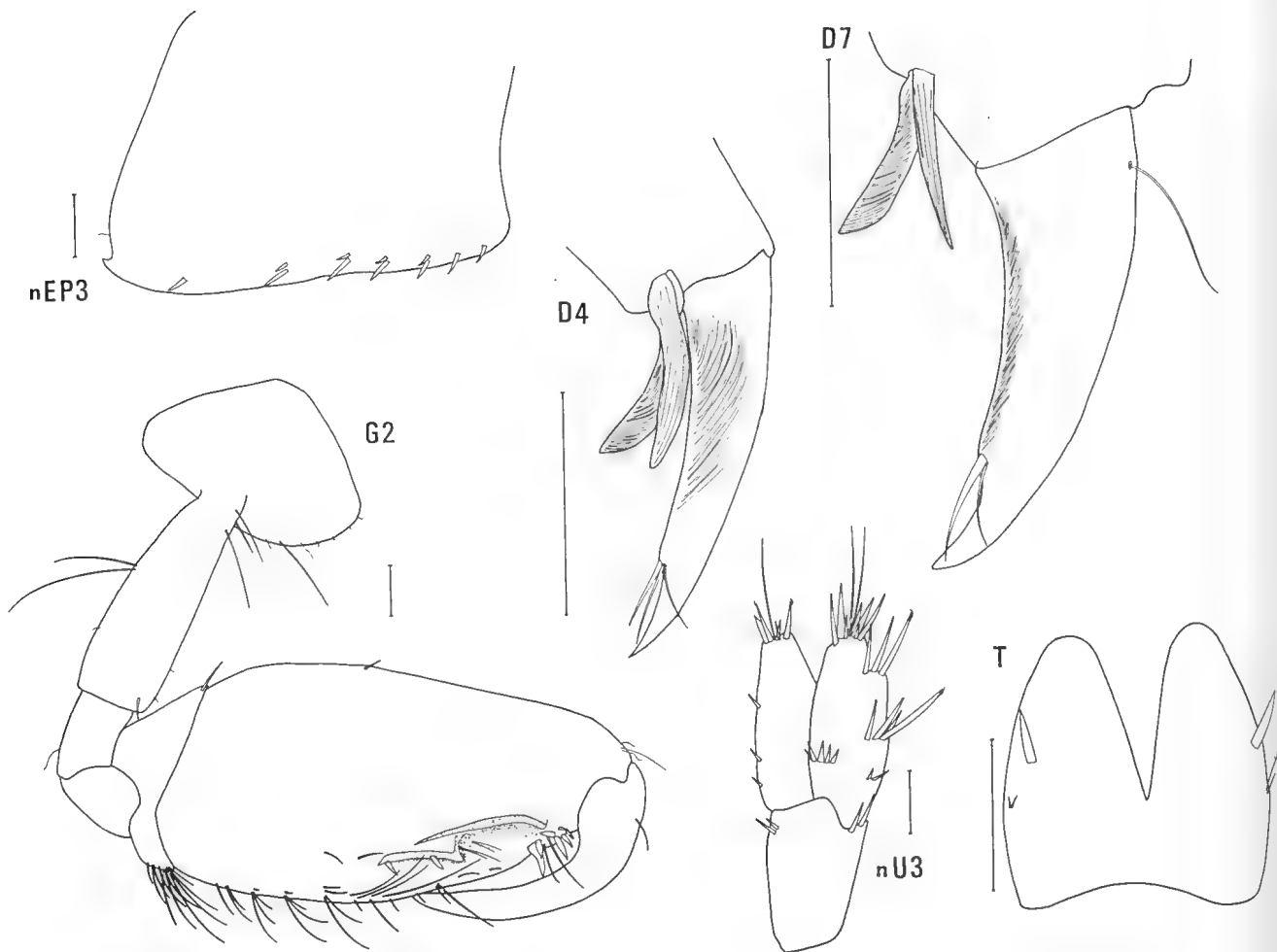


Fig. 14. *Elasmopus pocillimanus* (Bate), male, 4.9 mm, 76 LIZ 16; n = male, 7.2 mm, 76 LIZ 16. Scale lines represent 0.1 mm.

"is about 3-articulate". My material has 3 articles in the accessory flagellum.

There were no females in the material examined. Female *E. pocillimanus* are not known from the Indo-Pacific since Schellenberg (1938) and J.L. Barnard (1970, 1971) also did not find any females in the collections they examined.

Elasmopus pocillimanus was collected from shallow water at Lizard Island and from the reef back at Yonge Reef. It was found in dead staghorn *Acropora* coral and in reef rock covered with coralline algae *Lithothamnion* and *Halimeda*.

Distribution. Mediterranean (type locality, Genoa); Bermuda; Gilbert Islands; Hawaii; Madagascar; Cuba; Lizard Island; Yonge Reef.

Elasmopus pseudaffinis Schellenberg, 1938

Figs 15, 16

Elasmopus pseudaffinis Schellenberg, 1938:53-54, fig. 25.— J.L. Barnard, 1965:501-503, figs 12, 13; Ledoyer, 1972:219-222, pls 38, 39; 1978:273, fig. 29; 1979:73.

Material. AM P30114 and AM P30115 from the following stations: LI-50 (4), LI-62 (5).

Diagnosis. Accessory flagellum 3-4 articles; article 5 of gnathopod 2 compressed, posterior lobe setose; article 6 of male gnathopod 2 elongate, oblique palm confluent with posterior margin, defined by a stout spine, palmar margin with stout spines, distal protrusion spinous, submarginal spines stout; article 6 of pereopods 3 and 4 with distal pair of unstriated locking spines comprising one stout chisel spine and one curved spine; article 6 of pereopods 5-7 with distal pair of locking spines comprising 2 unstriated simple spines; third pleonal epimeron with posterventral cusp, posterior margin entire; telson longer than wide, cleft almost to base, apices notched with 1-3 stout spines at base of each notch.

Description. Male 11.5 mm. Head as long as first two pereonites, eye not filling lobe, ommatidia close-packed, cheek notch narrow. Antenna 1: peduncle equal to antenna 2; article 1 equal to article 2, with distal spine, article 3, 0.4 times as long as article 2; accessory flagellum 1.8 times as long as article 1 of primary

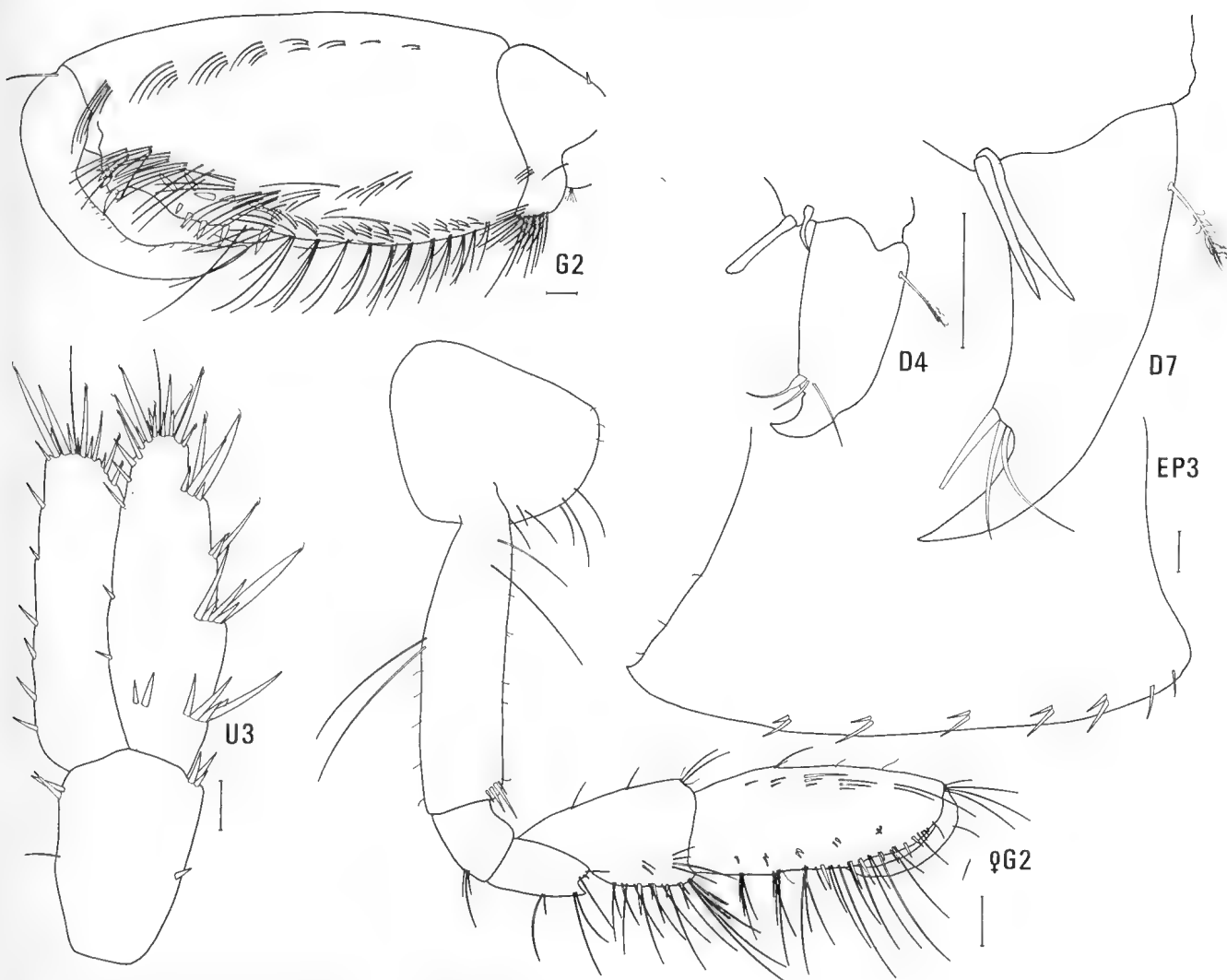


Fig. 15. *Elasmopus pseudaffinis* Schellenberg, male, 11.5 mm, LI-62; female = 7.1 mm, LI-62. Scale lines represent 0.1 mm.

flagellum, 4-articulate, article 4 small. *Antenna 2*: peduncle longer than flagellum, article 3 longest, article 4 subequal to article 3; flagellum 12-articulate.

Mandible with incisor and 3 accessory blades; lacinia mobilis bifid; molar triturating with long ragged setae; palp 3-articulate, article 2 twice as long as article 1, article 3 falcate with comb-like row of medial setae.

Maxilla 1: inner plate with 2 terminal plumose setae and fine marginal setae; outer plate broad, armed with 7 barbed spine teeth; palp 2-articulate, distally setose.

Maxilla 2: inner and outer plates with distal setae, outer plate with fine medial and marginal setae. *Maxillipeds*: inner and outer plates with plumose apical and marginal setae; palp 4-articulate, article 2 twice as long as articles 1, 3 and dactylus, pincushion lobe at articulation of article 3 and dactylus.

Gnathopod 1: coxa as long as wide, anteroventral corner slightly produced and smoothly rounded, ventral margin sparsely setose; article 5 anterior margin almost twice as long as posterior margin, posterior margin densely setose with some pectinate setae, 3 medial comb

rows of setae; article 6 almost twice as long as wide, posterior margin setose, 2 superior medial comb rows of setae, 4 inferior medial comb rows of setae, oblique palm defined by 2 stout spines, palm with submarginal setae and spines; dactylus extending length of palm. *Gnathopod 2* larger, more robust than gnathopod 1; coxa rounded, almost as wide as long with sparse ventral setae; article 2, 1.7 times as long as coxa; article 5 compressed with small spine on anterior margin, posterior margin densely setose; article 6 elongate, posterior margin with tufts of setae, superior medial setae short, inferior medial setae extending across palm, palm confluent with posterior margin, defined by a stout spine, palmar margin with 4 stout spines, distal spinous protrusion and 6 stout submarginal spines; dactylus stout, inner margin sparsely setose.

Peraeopods 3 and 4 similar except coxa 3, 1.4 times as long as wide. *Peraeopod 4*: coxa quadrate, posterior margin shallowly excavate; article 5 posterior margin spinous; article 6 posterior margin spinous, distal pair of locking spines comprising one stout chisel spine and

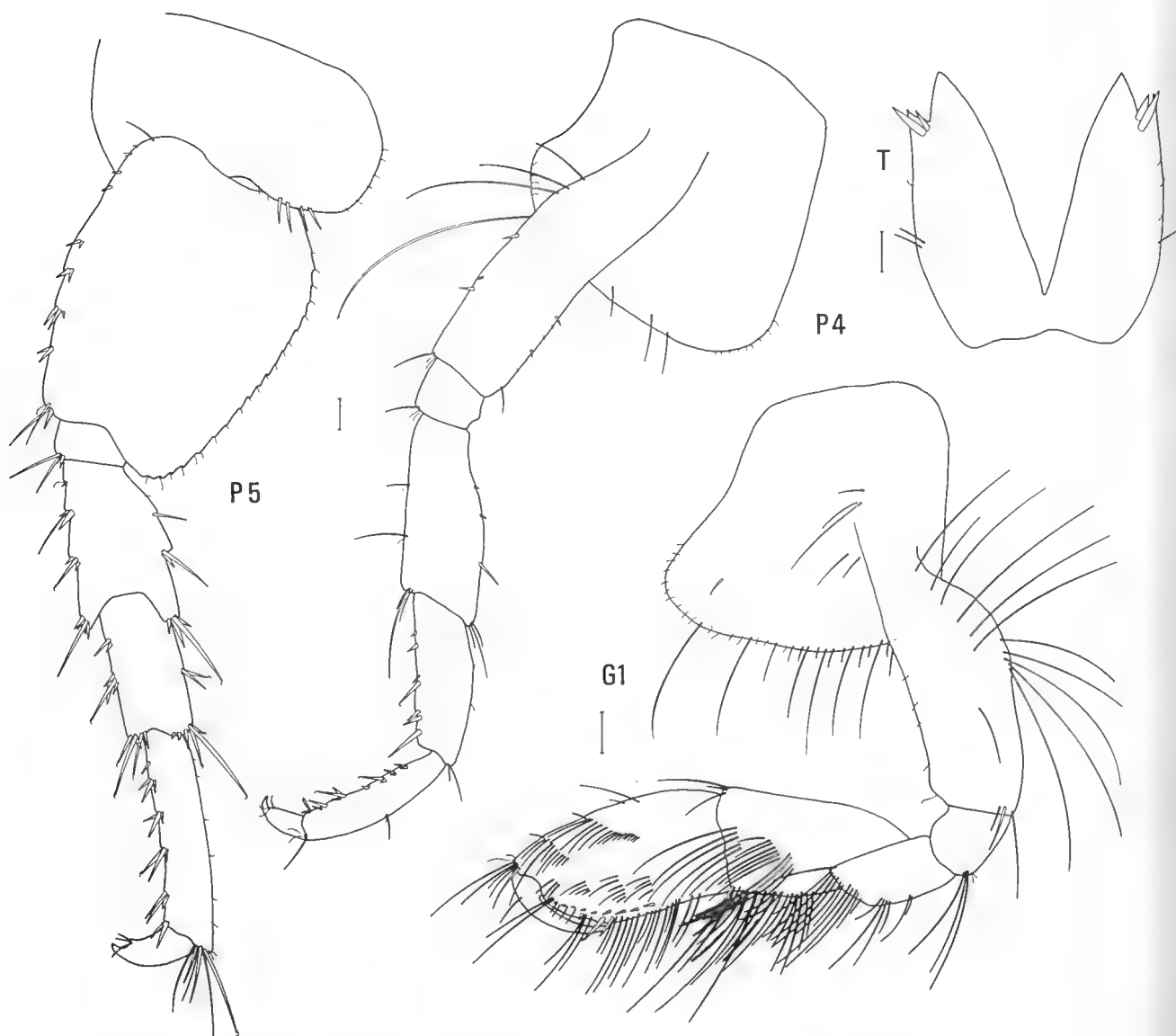


Fig. 16. *Elasmopus pseudaffinis* Schellenberg, male, 11.5 mm, LI-62. Scale lines represent 0.1 mm.

one curved spine; dactylus apically constricted, inner margin bearing seta and 2 setules at constriction. *Peraeopod 5*: coxa 1.6 times as wide as long, bilobed ventrally, 4 spines and sparse setae on posteroventral margin; article 2, anterior margin spinous, posterior margin weakly serrate, sparsely setose and lacking long setae; article 4 widening distally, anterior and posterior margins spinous and produced downwards; article 5 subequal to article 4, anterior and posterior margins spinous; article 6, 1.5 times as long as article 5, anterior margin spinous, distal pair of locking spines comprise 2 simple spines; dactylus apically constricted inner margin bearing a seta and 2 setules at constriction. *Peraeopod 6*: very similar proportions to peraeopod 5 but 1.7 times as long; coxa bearing 2 posteroventral spines; articles 2, 3, 4, 5 and 6 more spinous and setose than peraeopod 5. *Peraeopod 7*: very similar to peraeopod 6 in size and proportion.

Third pleonal epimeron with posteroventral cusp, ventral margin bearing 5 pairs of spines and 2 single spines anteriorly, posterior margin entire.

Uropod 3: peduncle 0.7 times as long as outer ramus, distal margins spinous; outer ramus ovate, apically spinous with a seta, outer margin armed with groups of spines, inner margin armed with single spines, 2 medial spines at M15; inner ramus subequal to outer ramus, apically spinous with a seta, outer margin armed with single spines. *Telson* longer than wide, cleft almost to base, apices notched with 2 stout spines at base of each notch.

Female 7.1 mm. Similar to male except in following ways: *Gnathopod 1* less robust and less setose. *Gnathopod 2* less robust; coxa 0.8 times as wide as long; article 2, 1.4 times as long as coxa; article 5 not compressed, posterior margin 0.5 times as long as anterior margin, spine on anterior margin absent.

posterior margin with tufts of setae; article 6 extremely elongate with short superior medial setae and inferior medial spines, stout spine distal to defining spine, palm with spines and setae, lacking distal protrusion.

Variation. *Gnathopod 1* less setose in smaller males; *Gnathopod 2* in smaller males, articles 5 and 6 less setose and less spinous; *Peraeopod 4*: articles 5 and 6 may be more or less setose than in peraeopod 4 figured, independent of size of male; *Peraeopod 6 and 7*: in smaller males, article 6 is less spinous; *Telson*: in both males and females, the larger apical spine may be up to twice the size of that figured. *Uropod 3*: the number of spines in each group of spines is variable, independent of the size of the specimen.

Remarks. J.L. Barnard (1965) found considerable variation amongst the specimens in the Micronesia collection, and he mentions the third pleonal epimeron in particular. The specimens examined from the Great Barrier Reef do not show such variation. The third pleonal epimeron of males, females and juveniles is produced posteroventrally to form a cusp. Schellenberg (1938) figures a notched posteroventral corner and J.L. Barnard (1965) refers to a "small sharp tooth" enclosed in the notch, but these characters are not observed in the material I examined.

Schellenberg (1938) described the palm of the male second gnathopod with a distal conical tooth and a more proximal truncate tooth bearing two spines. The specimen he described is 5 mm long. J.L. Barnard (1965) also figured the second gnathopod of a male 5 mm in length and showed a similar arrangement of teeth on the palm, although the distal tooth is truncate rather than conical. J.L. Barnard (1965) figured the second gnathopod of a 9 mm male and it appears that in larger specimens the truncate tooth is not as prominent and the entire palmar margin is more spinous. The male described from the Great Barrier Reef is 11.5 mm in length and the palm is like that of J.L. Barnard's 9 mm specimen. The smaller males examined (4.4 mm and 6.4 mm) have only a distal conical tooth and a spinous palmar margin. The margin is not as spinous as that of the 11.5 mm male of J.L. Barnard's 9 mm male.

J.L. Barnard (1965) noted that female *E. pseudaffinis* are indistinguishable from *Elasmopus minimus*, found by Chevreux (1907) and Pirlot (1936). But the third uropod of *E. minimus* has the inner ramus "beaucoup plus courte" than the outer ramus (Chevreux, 1907), and *E. pseudaffinis* has subequal rami of uropod 3.

J.L. Barnard (1965) identified the females in his collection as *E. pseudaffinis* because they were always found in conjunction with males with the second gnathopodal configuration of *E. pseudaffinis*. This was the case in the material examined but the identification of the females was confirmed by the rami of uropod 3.

Ledoyer (1978) described two forms of *E. pseudaffinis* based on coxa 1. Form A has a smoothly rounded anteroventral corner and Form B has a sharp anteroventral corner. Ledoyer (1978) also noted that Form A from Madagascar and Form B from Mauritius have a strong spine on the posteroventral corner of

coxae 1-3. The material examined fits Form A from Mauritius since the anteroventral corner of coxa 1 is smoothly rounded and it lacks a spine on the posteroventral corner of coxae 1-3.

Elasmopus pseudaffinis was found in algal samples from shallow water at Lizard island and Eagle Reef.

Distribution. Micronesia (type locality, Gilbert Islands); Madagascar; Mauritius; Lizard Island; Eagle Reef.

Elasmopus spinicarpus n.sp.

Figs 17, 18, 19

Type material. HOLOTYPE, male, 8.5 mm, AM P30212; ALLOTYPE, 5.4 mm, AM P30213; 33 PARATYPES, AM P30214; Casuarina Beach, Lizard Island (14°40.5'S, 145°26.6'E) under stones at low tide mark, J.K. Lowry, A.R. Jones and P.C. Terrill, 11 October 1978, L1-39.

Diagnosis. Accessory flagellum 3-articulate; coxae 1-4 large; article 5 of male gnathopod 2 with long setae arising medially, 5 spines anteroventrally; article 6 of male gnathopod 2 tapering distally, oblique palm confluent with posterior margin, defined by 2 stout spines, palmar margin with spines, setae and submarginal spines; article 6 of peraeopods 3 and 4 with distal pair of unstriated locking spines comprising one chisel spine and one simple curved spine; article 6 of peraeopods 5-7 with distal pair of locking spines simple, comprising one stout spine and a smaller curved spine; third pleonal epimeron with posteroventral cusp, posterior margin entire; telson wider than long, deeply cleft, outer margins of lobes extended to form apical points, each with 3 apical spines.

Description. Holotype, male, 8.5 mm. *Head* 0.7 times as long as first two peraeonites, eye not filling lobe, ommatidia close-packed, cheek notch narrow. *Antenna 1* twice as long as antenna 2; peduncle equal to flagellum, article 1 subequal to article 2, with distal spine, article 3, 0.6 times as long as article 2; flagellum 17-articulate; accessory flagellum 0.8 times as long as first article of primary flagellum, 3-articulate, article 3 small. *Antenna 2*: peduncle longer than flagellum, article 4 longest, article 3 subequal to article 4; flagellum 8-articulate.

Mandible with incisor and 3 accessory blades; lacinia mobilis with 4 teeth; molar triturating; palp 3-articulate, article 2 twice as long as article 1, article 3 falcate with comb-like row of medial setae. *Maxilla 1*: inner plate with 2 terminal plumose setae and fine marginal setae; outer plate broad, armed with 7 barbed spine teeth; palp 2-articulate, distally setose. *Maxilla 2*: inner and outer plate with distal setae, outer plate with fine median and marginal setae. *Maxillipeds*: inner and outer plates with plumose apical and inner marginal setae; palp 4-articulate, article 2 twice as long as articles 1, 3 and 4, pincushion lobe at articulation of article 3 and dactylus.

Gnathopod 1: coxa 0.8 times as wide as long, ventral margin sparsely setose; article 5, anterior margin twice

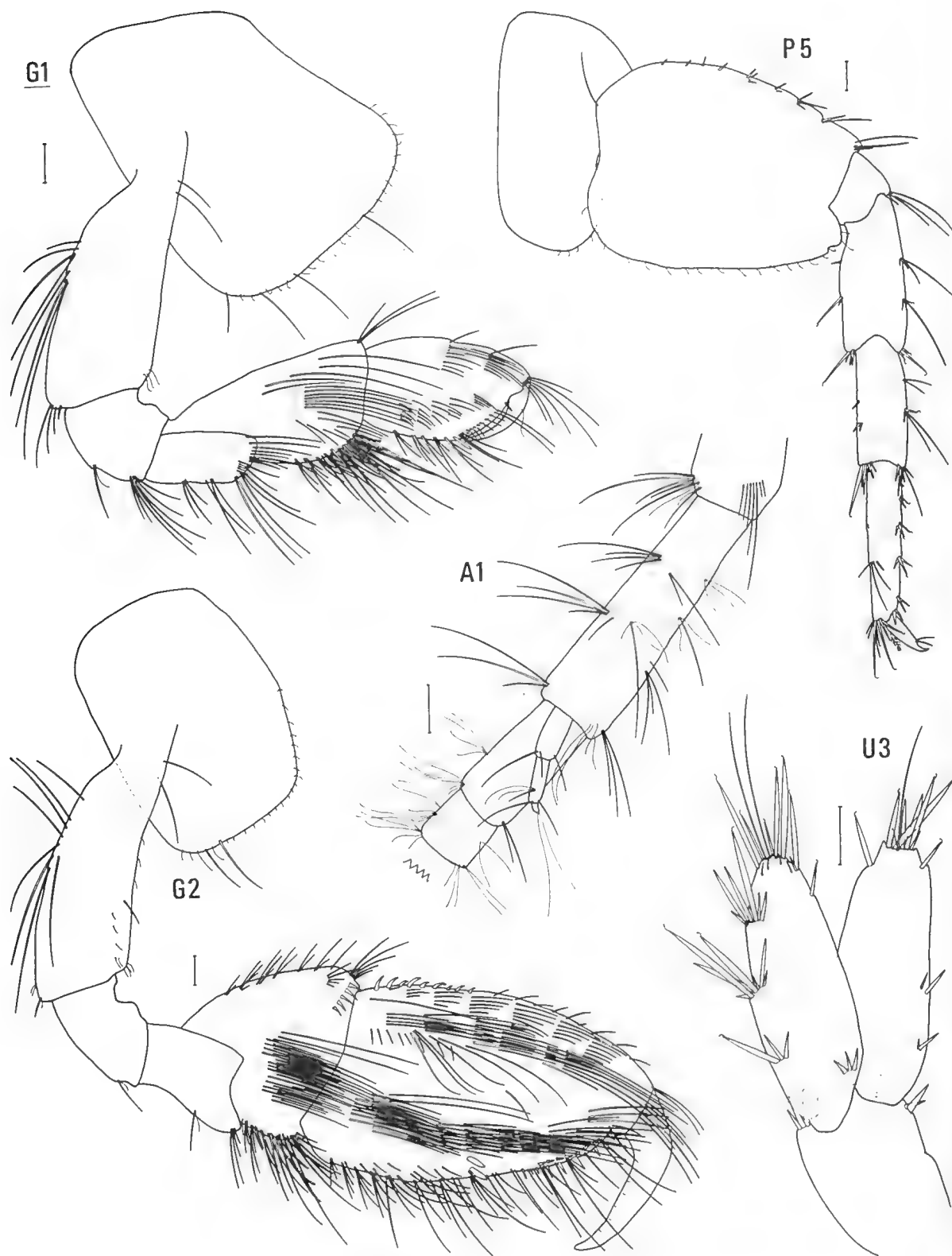


Fig. 17. *Elasmopus spinicarpus* n.sp., holotype, male 8.5 mm, L1-39. Scale lines represent 0.1 mm.

as long as posterior margin, posterior margin densely setose with some pectinate setae, long setae arising medially; article 6 ovate, 1.6 times as long as wide, posterior margin with tufts of setae, 2 rows superior medial setae, 5 rows inferior medial setae, oblique palm

defined by stout spine, palm with short setae, submarginal spines and one distal spine; dactylus extending almost length of palm. *Gnathopod 2* larger, more robust than gnathopod 1; coxa rectangular, 0.7 times as wide as long, ventral margin and distal half of

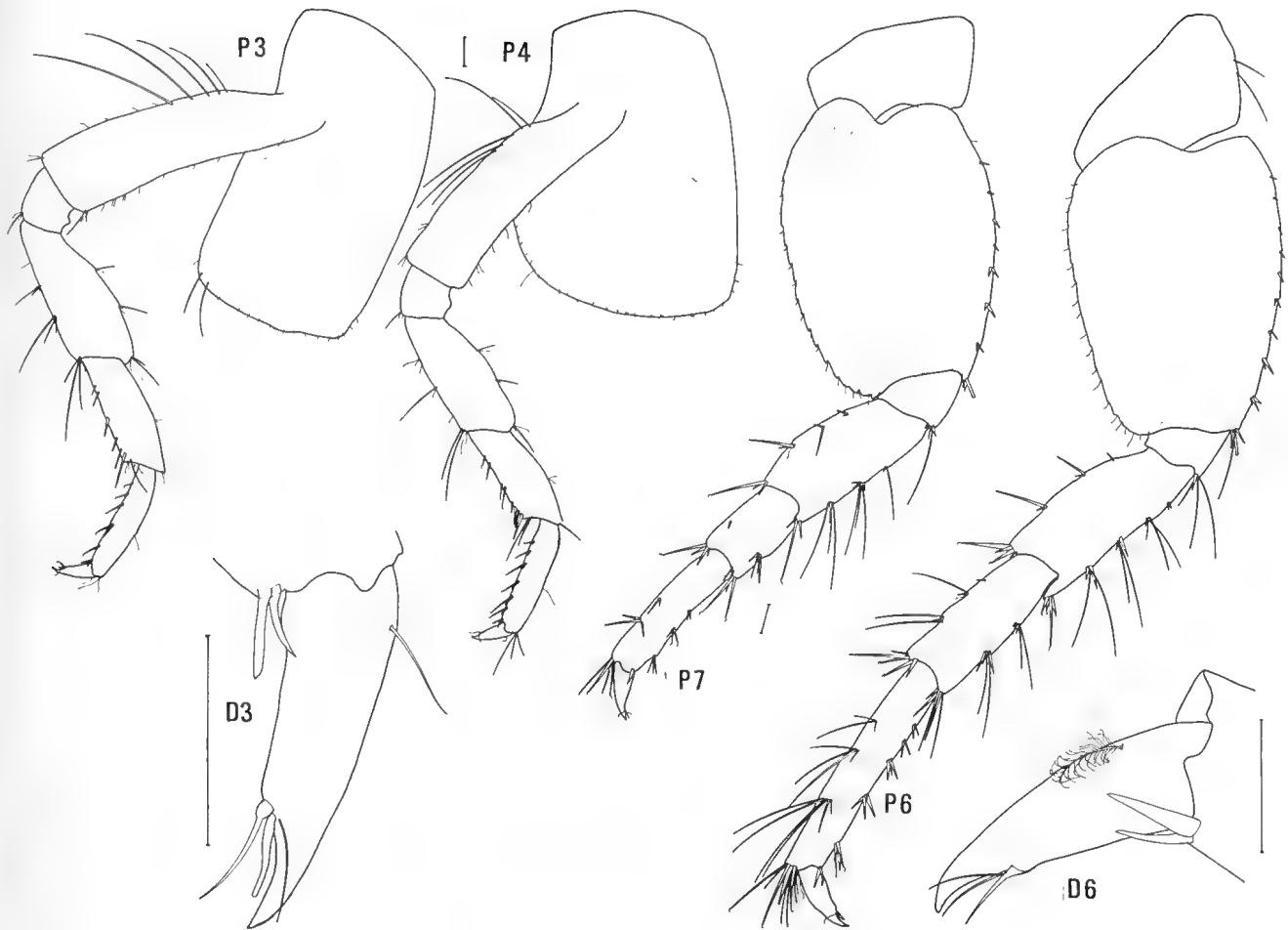


Fig. 18. *Elasmopus spinicarpus* n.sp., holotype, male 8.5 mm, L1-39. Scale lines represent 0.1 mm.

anterior margin sparsely setose; article 2 equal in length to coxa; article 5 posterior margin 0.4 times as long as anterior margin, anterior margin with tufts of setae, 5 spines anteroventrally, posterior margin densely setose, long setae arising medially; article 6 tapering distally, long setae arising proximally spinous, posterior margin setose, superior medial setae and inferior medial setae long and fine, oblique palm confluent with posterior margin, defined by 2 stout spines, palmar margin with spines, setae and submarginal spines; dactylus slender, inner margin sparsely setose.

Peraeopod 3: coxa large, rectangular, 1.7 times as long as wide; article 2, 0.8 times as long as coxa; article 5 posterior margin spinous; article 6 posterior margin spinous, distal pair of unstriated locking spines comprising one chisel spine and one curved spine; dactylus apically constricted, inner margin bearing seta and two setules at constriction. **Peraeopod 4** very similar in size and proportions to peraeopod 3 except in following ways: coxa wider than coxa 3, 1.3 times as long as wide, posterior margin produced posteriorly to form cusp; articles 5 and 6 more spinous. **Peraeopod 5:** coxa, 1.5 times as wide as long, bilobed ventrally; article 2 anterior margin spinous, posterior margin entire; sparsely setose and lacking long setae; articles

4, 5 and 6 rectangular, anterior and posterior margins spinous, article 5 subequal to articles 4 and 6; article 6, distal pair of locking spines simple, comprising one stout spine and a smaller curved spine; dactylus apically constricted, inner margin bearing seta and 2 setules at constriction. **Peraeopod 6:** similar proportions to peraeopod 5 but 1.2 times as long; coxa not bilobed ventrally; article 2 posterior margin weakly serrate; article 4 anterior and posterior margins produced downwards; articles 4, 5 and 6 more setose and spinous. **Peraeopod 7:** similar proportions to peraeopod 6 but same size as peraeopod 5; article 2 more strongly serrate; articles 4, 5 and 6 less setose and spinous.

Third pleonal epimeron with posteroventral cusp and single spines along ventral margin, posterior margin entire.

Uropod 3: peduncle 0.6 times as long as outer ramus, distal margin spinous; outer ramus ovate, apically spinous with 2 setae, outer margin armed with groups of spines, 3 medial spines at M19; inner ramus ovate, subequal to outer ramus, apically spinous with a seta, inner margin spinous. **Telson** deeply cleft, wider than long, outer margins of lobes extended to form apical points each with 3 small spines.

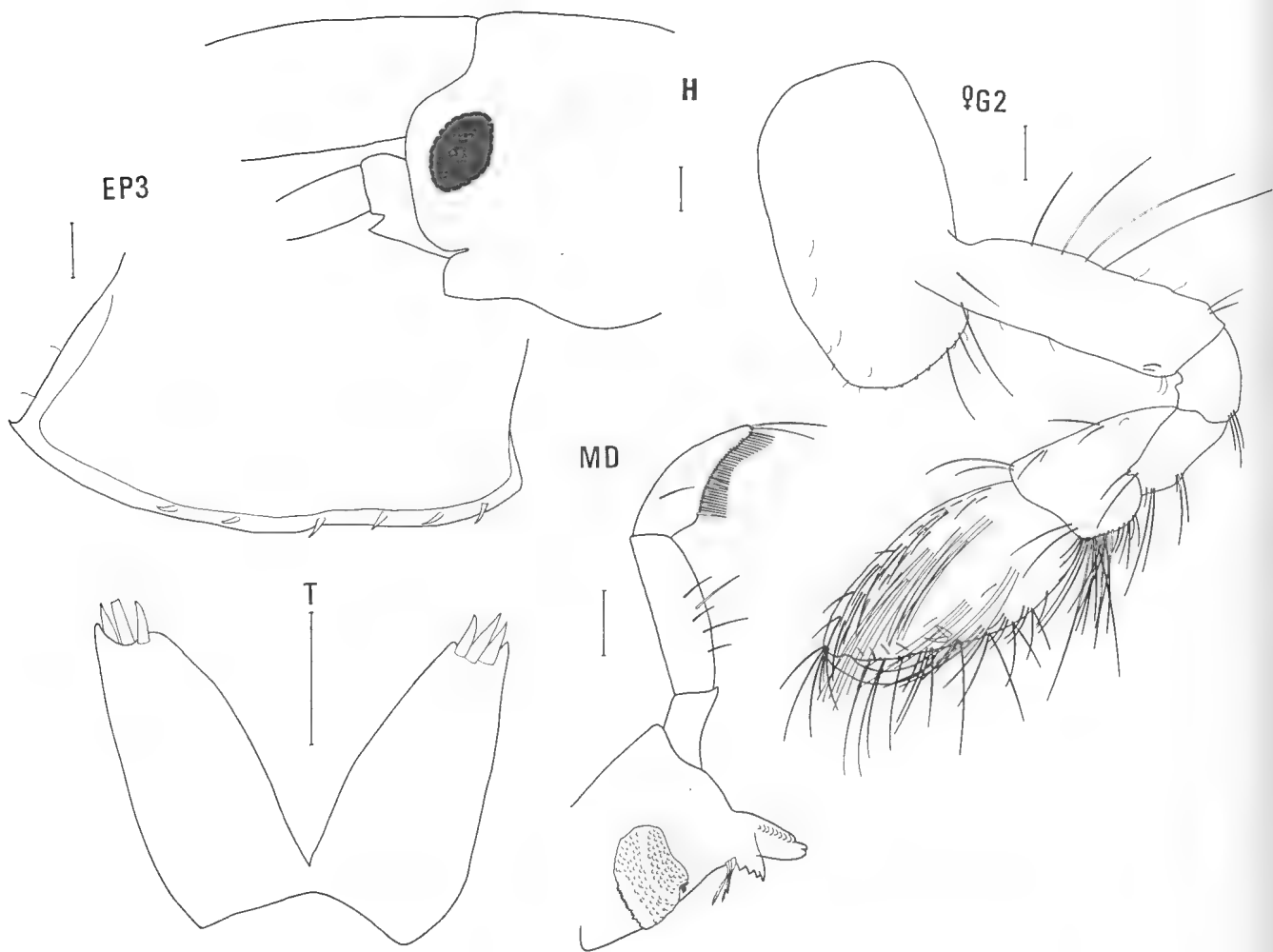


Fig. 19. *Elasmopus spinicarpus* n.sp., holotype, male 8.5 mm, LI-39; female = allotype, 5.4 mm, LI-39. Scale lines represent 0.1 mm.

Allotype female, 5.4 mm. Similar to holotype except in following ways: *Gnathopod 1*: article 6, fewer superior and inferior medial setae. *Gnathopod 2* smaller and less robust, coxa 0.6 times as wide as long; article 2, 0.8 times as long as coxa; article 5 posterior margin 0.3 times as long as anterior margin, lacking long medial setae and anteroventral spines; article 6 lacking spines on anterior margin, palmar margin less spinous, lacking submarginal spines. *Peraeopods 3 and 4*: article 6 less spinous. *Peraeopod 6* less setose. *Telson*: middle apical spine more than twice as long as others.

Remarks. The specific epithet *spinicarpus* (L. *spina* = a spine; *carpus* = article 5) refers to the spines along the ventral margin of article 5 of the male second gnathopod.

Elasmopus spinicarpus resembles *E. brasiliensis* (Dana) in the plain but setose article 6 of the male second gnathopod figured by Chevreux (1910). The anterior margin of article 5 of the second gnathopod of *E. spinicarpus* is more setose than *E. brasiliensis*, and *E. brasiliensis* lacks spines along the ventral margin. J.L. Barnard (1965) recorded *E. brasiliensis* from Micronesia, and noted that the palm of the male second

gnathopod has a distal pair of spines and a chitinous ridge on the medial face. These features are not present on *E. spinicarpus*.

The telson of *E. brasiliensis* was not figured by Chevreux (1910) but he stated that it is wider than long, almost entirely cleft, with excavate apices armed with 3 unequal spines. From this description, the telsons of *E. spinicarpus* and *E. brasiliensis* appear similar.

Elasmopus spinicarpus has rami of uropod 3 equal, which is similar to the third uropod of *E. bampo* Barnard, from Hawaii and California (J.L. Barnard 1979). *E. bampo*, however, has the posterior margin of the third pleonal epimeron serrate, whereas *E. spinicarpus* has the posterior margin entire.

Elasmopus spinicarpus occurred in one sample which was taken from under stones at low tide. Of the 35 specimens collected, 16 were ovigerous females.

Distribution. Lizard Island (type locality).

Genus *Maera* Leach

Six species of *Maera* have previously been recorded in Australia. Sheard (1937) listed four species from

temperate Australia—*M. inaequipes* (Costa), *M. hamigera* (Haswell), *M. mastersi* (Haswell), and *M. tenella* (Dana). *Maera tenella* was reported from the Abrolhos Islands by Tattersall (1922) but according to Schellenberg (1938) the species was *M. serrata*.

Maera viridis (Haswell) is described by Haswell (1880b) from Port Jackson and also recorded by J.L. Barnard (1972) from a number of localities in southern Australia. *Maera boeckii* was described by Haswell (1879) from Port Jackson. Sheard (1937) listed *M. viridis* and *M. boeckii* in the genus *Elasmopus*.

Five species of *Maera* are found in the material from Lizard Island and adjacent reefs. *Maera quadrimana* (Dana), *M. octodens* Sivaprakasam and *M. reishi* Barnard are new records for Australia. *Maera serrata* is recorded from the east coast for the first time. However, on examination of the Melitidae in the British Museum (Natural History) from the Great Barrier Reef Expedition, it was found that *M. serrata* was collected at Low Isles. This record was published as *Maera* sp. by K.H. Barnard (1931). One new species, *M. griffini*, is described.

The five species fall into two groups. *Maera quadrimana*, *M. serrata* and *M. reishi* are in the "quadrimana complex" discussed by J.L. Barnard (1972b). They are characterized by the transverse palm on gnathopod 2, an accessory tooth on the dactylus of peraeopods, and by a sharp cusp at the anteroventral cephalic corner. *Maera griffini* and *M. octodens* have an oblique palm on gnathopod 2, lack an accessory tooth on the dactylus of peraeopods, and lack the sharp cusp at the anteroventral cephalic corner.

Maera griffini n.sp.

Figs 20, 21

Type material. HOLOTYPE, male, 8.6 mm, AM P30205; 5 PARATYPES, AM P30206, fringing reef, between Bird Islet and South Island, Lizard Island (14°42'S, 145°28'E), air lifted sediment, 12 m depth, P.B. Berents and P.M. Berents, 14 April 1978, 78 LIZ-PBW-2.

Additional material. AM P30207 and L1-59 (1).

Diagnosis. Head with anteroventral cephalic corner quadrate, lacking cheek notch; coxa 1 anteroventral corner drawn to subacute point, posteroventral corner notched; gnathopods 2 symmetrical; male gnathopod 2 palm oblique defined by sharp tooth, incision adjacent to defining tooth, shallow sinus midway along palm, palmar margin with large stout spines and small spines; dactylus of peraeopods lacking accessory tooth; third pleonal epimeron posterior margin entire; uropod 3 rami lanceolate, equal, 1.6 times as long as peduncle; telson wider than long, deeply cleft, apices notched bearing 2 setae longer than telson, inner margins with notch bearing 2 setae.

Description. Holotype male, 8.6 mm. Head as long as first 2 peraeonites, lateral cephalic lobe strongly produced anteriorly, eye tear-drop shape, not filling lobe, ommatidia close-packed, anteroventral cephalic

corner quadrate, lacking cheek notch. *Antenna 1*: flagellum longer than peduncle, peduncular article 2 subequal to article 1, distal border with stout spine, article 3 small; flagellum 24-articulate; accessory flagellum 4-articulate, article 4 small. *Antenna 2*: peduncle longer than flagellum, article 2 gland cone extending length of article 3; flagellum 17-articulate.

Mandible with well developed incisor and 8 accessory blades comprising 4 serrated spines and 4 plumose setae; lacinia mobilis with 4 teeth; ragged seta and 4 short setae extending from triturating molar; palp slender, 3-articulate, article 3 with 8 apical setae. *Maxilla 1*: inner plate with 3 terminal plumose setae and fine marginal setae; outer plate armed with 4 serrate and 5 bifid spine teeth; palp 2-articulate, distally setose. *Maxilla 2*: inner and outer plates with distal setae; outer plate with fine marginal setae. *Maxillipeds*: inner plate quadrate with plumose apical setae; outer plate ovate with apical spine teeth extending along inner margin; palp 4-articulate, inner margin article 2 setose, article 3 with inner marginal and apical setae.

Gnathopod 1: coxa as wide as long, strongly produced anteriorly, anteroventral corner drawn to subacute point, setae spaced along ventral margin, posteroventral corner notched; article 4 distally setose, tapering to a point, posterior margin armed with row of sharp spines; article 5 posterior margin densely setose, medial face covered with comb rows of long setae including distal row of pectinate setae; article 6 elongate, tapering distally, subequal to article 5, posterior margin setose with submarginal spines, oblique palm confluent with posterior margin, palmar margin bearing setae and spines, superior medial setae long, inferior lateral setae short; dactylus slender, inner margin setose. *Gnathopod 2*: larger and more robust than gnathopod 1; coxa as wide as long; ventral margin sparsely setose; article 2, 0.4 times as wide as long, anterior margin sparsely setose, posterior margin bearing long setae; article 4 posteroventral corner acute; article 5 compressed, anteroventral corner bearing 2 spines, posteroventral margin densely setose with some pectinate setae, row of setae along mid-ventral margin; article 6 robust, widening distally, tufts of setae spaced along ventral margin, oblique palm defined by sharp tooth, incision adjacent to defining tooth, shallow sinus midway along palm, palmar margin armed with large stout spines and small spines; dactylus curved, inner margin setose.

Peraeopod 3: coxa 0.8 times as wide as long, ventral margin setose, posteroventral corner with small sharp tooth; article 4 anteroventral corner broad; article 6 subequal to article 5, posterior margin spinous with distal pair of simple locking spines; dactylus apically constricted, constriction marked by 2 setules and notched protrusion, plumose seta medial to outer margin. *Peraeopod 4* similar proportions to peraeopod 3 but shorter; coxa has shallow excavation of posterior margin. *Peraeopod 5*: coxa 1.5 times as wide as long; article 2 ovate, 0.7 times as wide as long, proximal anterior margin spinous, distal anterior margin setose, proximal posterior margin setose, posteroventral corner

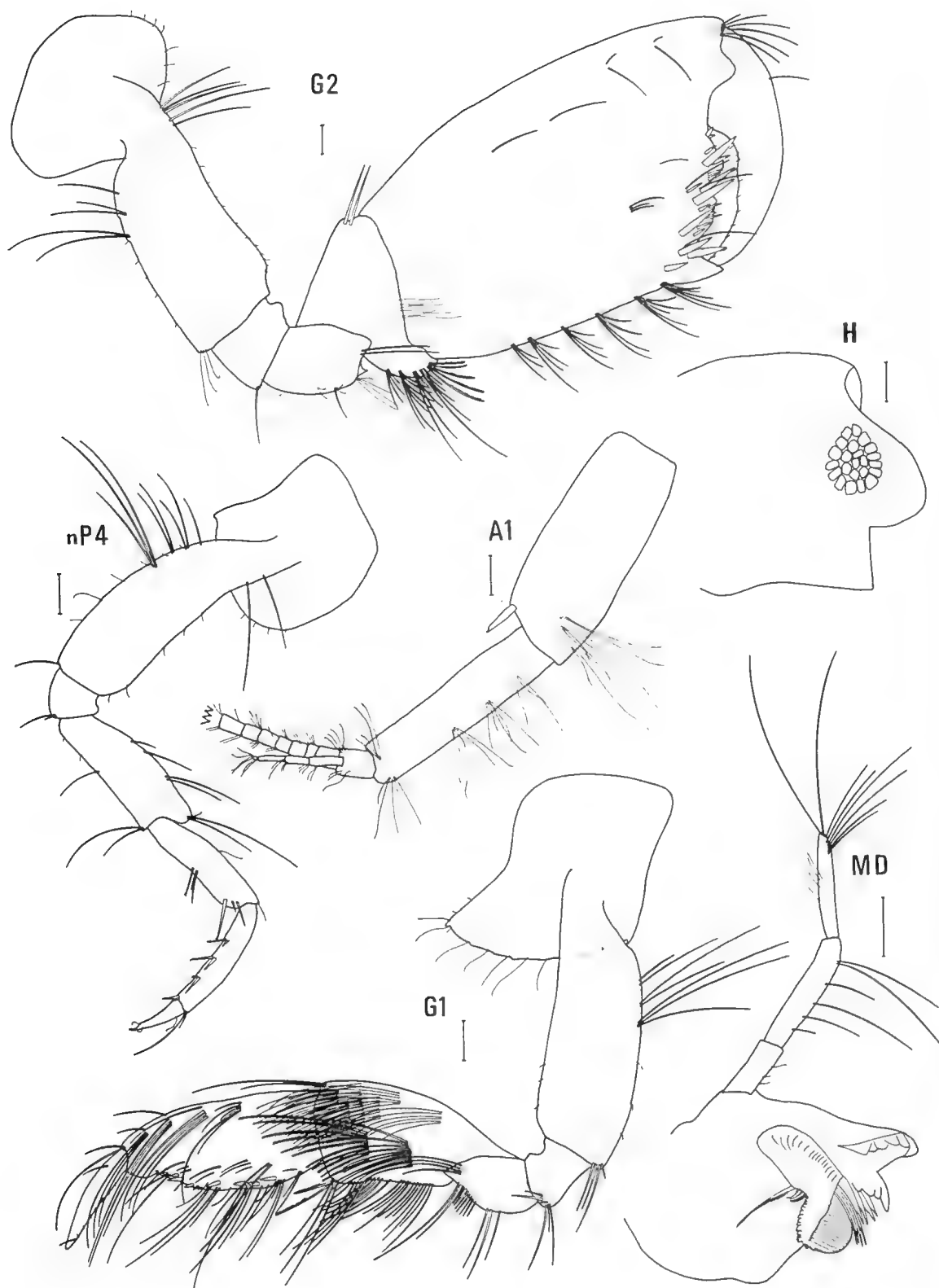


Fig. 20. *Maera griffini* n.sp., holotype, male, 8.6 mm, 78 LIZ-PBW-2; n = male, 7.2 mm, 78 LIZ-PBW-2. Scale lines represent 0.1 mm.

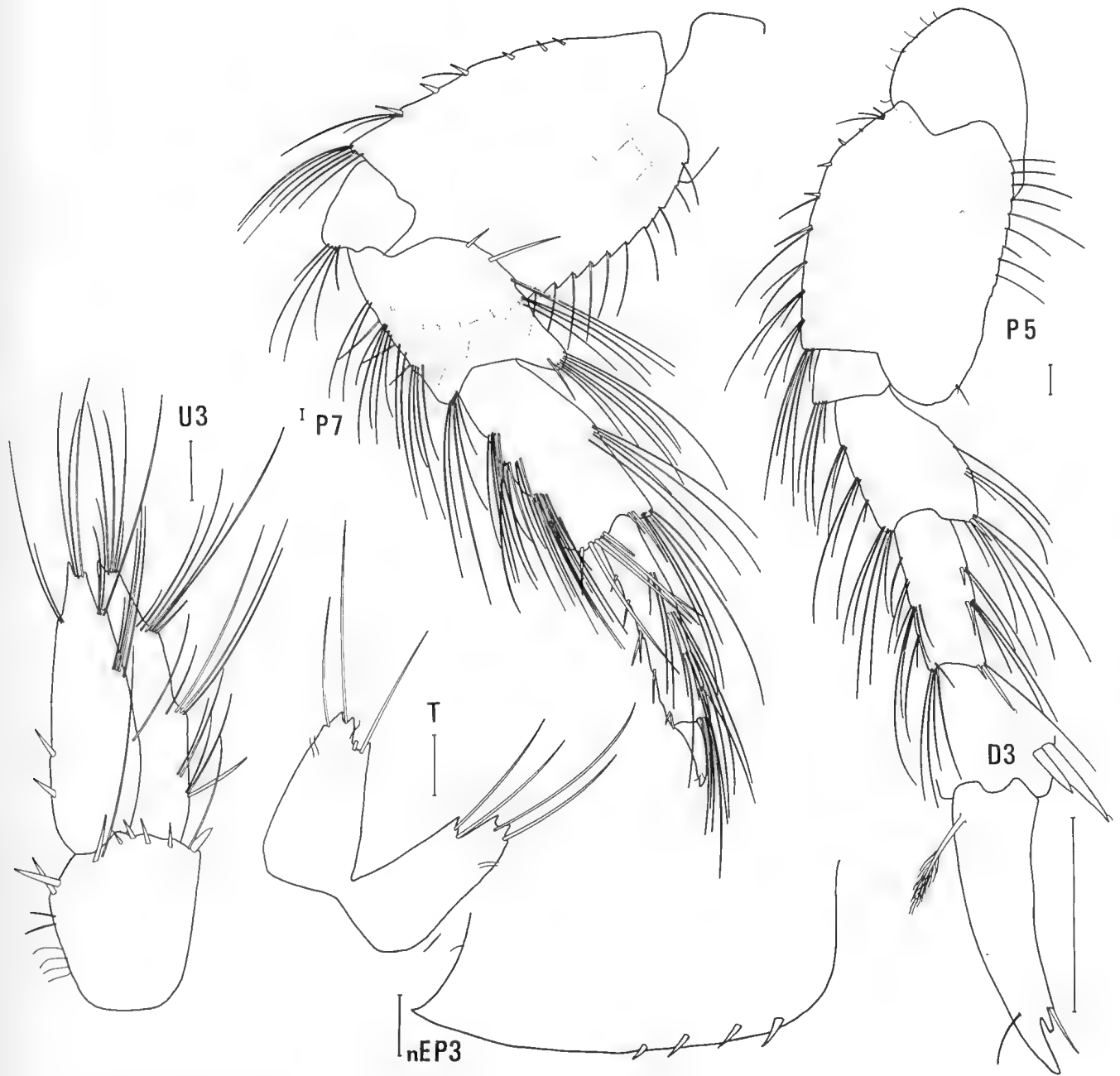


Fig. 21. *Maera griffini* n.sp., holotype, male, 8.6 mm, 78 LIZ-PBW-2; n = male, 7.2 mm, 78 LIZ-PBW-2. Scale lines represent 0.1 mm.

broadly expanded; article 4 posteroventral corner broad, anterior and posterior margins setose; article 5 rectangular, equal to article 4, anterior margin setose, posterior margin with tufts of setae and stout spines; article 6 subequal to article 5; dactylus apically constricted, constriction marked by 2 setules and notched protrusion, plumose seta medial to outer margin. *Peraeopod 6* very similar proportions to *peraeopod 5* but larger and more setose; article 2, posterior margin serrate and setose; article 4 stout spine from proximal posterior margin. *Peraeopod 7* very similar size and proportions to *peraeopod 6* except more setose; article 4, 2 stout spines on proximal posterior margin.

Third pleonal epimeron with posteroventral cusp, 4 spines projecting from ventral margin, anteroventral corner smoothly rounded, posterior margin entire.

Uropod 3 extending beyond uropods 1 and 2; peduncle 0.6 times as long as outer ramus, distal and inner margins spinous; both rami taper distally; outer ramus with apical setae, setae spaced along outer margin, apex acute; inner ramus equal to outer ramus with apical setae, setae along outer margin, apex acute, spines on proximal inner margin. *Telson* wider than long, deeply cleft, apex notched, sharp notch on inner margin proximal to apex, 2 apical setae longer than telson, 2 setae at proximal notch.

Female not known.

Variation. Smaller males show variation from the holotype in the following ways: palm of gnathopod 2 has less prominent defining tooth and shallower mid-palmar sinus; peraeopods 5-7 and uropod 3 less setose; telson has only 1 apical seta and 1 seta at the notch on inner margin.

Remarks. *Maera griffini* is named after Dr D.J.G. Griffin, Director of the Australian Museum.

Maera griffini shows some similarities with *M. othonopsis* Schellenberg from the Gilbert Islands, in the serrate article 2 of peraeopod 7 and in coxa 1 which is strongly produced anteriorly. However, article 2 of peraeopod 7 is not broadly expanded at the posteroventral corner, the posterior margin of the third pleonal epimeron is notched and the apices of the telson are blunt.

The profile of the head shows some variation within the genus *Maera* and *M. griffini* is similar to the European species *M. othonis* Milne Edwards, although the eye of *M. othonis* is shown by Chevreux and Fage (1925) to be reniform.

Another species that has some similar characters to *M. griffini* is *M. grossimana* (Montagu). This species has the anteroventral corner of coxa 1 extended anteriorly, notched apices of the telson and the posterior margin of the third pleonal epimeron entire; however, peraeopods 5-7 are more slender and the posterior margin of article 2 is not serrate.

Maera griffini was collected in air-lifted sediment from coral fans, rubble, dead coral and reef rock on the reef face and bommies at Lizard Island and Eagle Reef.

Distribution. Lizard Island (type locality); Eagle Reef.

Maera octodens Sivaprakasam, 1968

Fig. 22 in part

Maera octodens Sivaprakasam, 1968:36-38, fig. 2.—Surya Rao, 1972:196; Ledoyer, 1978:278, fig. 31; 1979:80, fig. 45.

Material. AM P30116 from L1-59(1).

Diagnosis. Head with anteroventral cephalic corner smoothly rounded, cheek notch present; coxa 1 anteroventral corner drawn to acute point, posteroventral corner notched; gnathopods 2 asymmetrical; male right second gnathopod palm oblique, 8 teeth form palmar margin; dactylus of peraeopods lacking accessory tooth; third pleonal epimeron posterior margin bearing 3 notches; uropod 3 rami elongate, subequal, 1.7 times as long as peduncle; telson longer than wide, deeply cleft, apices notched bearing long spine, inner margins with notch bearing spine.

Remarks. A single male of 4.8 mm was found in sediment from coral fans, rubble and dead coral at Eagle Reef. Although the specimen is damaged and lacking peraeopods 5-7, it is very similar to Sivaprakasam's (1968) description of a single male *M. octodens*.

The specimen varies from Sivaprakasam's (1968) description in the following ways: *Antenna 1*: the length of the peduncular joints in Sivaprakasam's specimen is in the ratio 2.8:3.2:1 whereas in this specimen it is in the ratio 4.2:4.5:1. The 4-articulate accessory flagellum extends to the fourth article of the primary flagellum compared with Sivaprakasam's (1968) specimen where it reaches the second article. *Right gnathopod 2*: article 6 is 1.5 times as long as wide whereas Sivaprakasam's (1968) specimen is twice as long as wide. Sivaprakasam (1968), however, does not define the parameters used in measuring the relative length of articles and different measurements may have been used in this comparison. In both specimens the right second gnathopod is large and well developed and the left underdeveloped.

Distribution. East coast of India (type locality, Appa Island); Mauritius; Madagascar; Eagle Reef.

Maera quadrimana (Dana, 1852)

Fig. 22 in part

Gammarus quadrimanus Dana, 1852:955-956, pl. 65, fig. 9.

Moera quadrimanus.—Bate, 1862:194-195, pl. 35, fig. 5.

Not Moera quadrimanus.—Thomson, 1882:235, pl. 17, fig. 4 (*vide* Schellenberg, 1938).

Maera quadrimana part.—Stebbing, 1906:434-435 (*vide* Schellenberg, 1938).

Maera quadrimana—Schellenberg, 1938:45-48, figs 21, 22; J.L. Barnard, 1955:13; 1962:99; 1965:511-512, fig. 17; 1970:152-153, figs 94, 95; 1971:77, 84, figs 38, 40; 1972b:107; Sivaprakasam, 1966:101-102; 1968:35; Ledoyer, 1972:229, pl. 45; 1978:279; 1979:80; Surya Rao, 1972:196; Ortiz, 1978:8.

Material. AM P30117 to AM P30122 from the following stations: 75 LIZ 1-5 (3), 76 LIZ A (13), 76 LIZ B (10), 76 LIZ 16 (2), L1-16 (3), L1-48 (1).

Diagnosis. Head with anteroventral cephalic corner produced as sharp cusp, lacking cheek notch; coxa 1 anteroventral corner smoothly rounded, posteroventral corner notched; gnathopods 2 symmetrical; gnathopod 2 palm transverse with defining tooth projecting beyond palmar margin, palmar margin spinous with 2 distal sinuses; dactylus of peraeopods with accessory tooth; third pleonal epimeron posterior margin entire; uropod 3 rami subequal, truncate, 1.2 times as long as peduncle; telson wider than long, deeply cleft, apices truncate bearing 4-5 spines.

Remarks. The fully developed palm of gnathopod 2 in both male and female *M. quadrimana* is transverse with 2 sinuses and 3 truncate processes, plus a sinus adjacent to the defining tooth. The 2 distal sinuses on the palm (i.e. not the sinus adjacent to the defining tooth) show considerable variation in development. Sivaprakasam (1966) found specimens of 3-4 mm with an evenly convex palm although J.L. Barnard (1970) figured a 3.3 mm male with the sinuses of the fully developed palm. J.L. Barnard (1970) also figured a 5.0 mm female lacking sinuses with an evenly convex palm.

In the material examined a male of 3.7 mm showed the sinuses beginning to develop and a 4.5 mm male

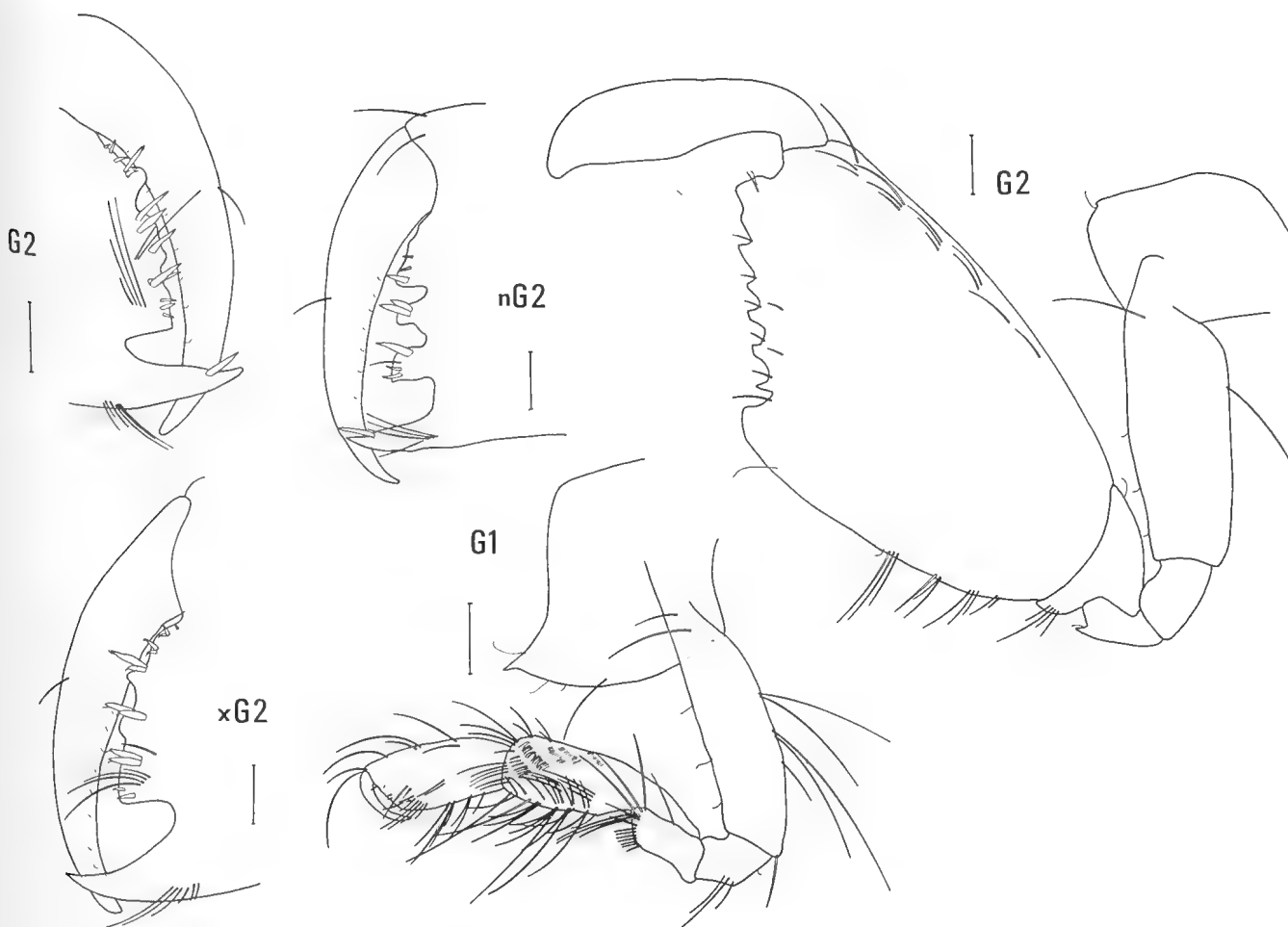


Fig. 22. Three illustrations at left: detail of palm of 2nd gnathopod, *Maera quadrimana* (Dana), female, 3.9 mm, 76 LIZ B; n = female, 5.4 mm, 76 LIZ B; x = female, 4.3 mm, 76 LIZ B. Two illustrations at right: *Maera octodens* Sivaprakasam, male, 4.8 mm, LI-59.

showed the fully developed palm. A female of 3.9 mm had a fully developed palm but females of 4.3 mm and 5.4 mm had palms with very shallow sinuses.

Maera quadrimana was collected in samples of reef rock, dead coral *Pocillopora*, algae including brown algae, *Dictyota* and green algae *Chlorodesmis*, coral rubble and silt from Lizard Island in depths up to 12 metres.

Distribution. Fiji (type locality); Micronesia; Gilbert Islands; Hawaii; Madagascar; Mauritius; Bay of Bengal; Cuba; Lizard Island.

Maera reishi Barnard, 1979

Fig. 23

Maera reishi J.L. Barnard, 1979:83-86, figs 45-47.

Material. AM P30094, AM P30159 and AM P30160 from the following stations: 75 LIZ 4-3 (1), 76 LIZ A (8), 76 LIZ B (16).

Diagnosis. Head with anteroventral cephalic corner produced as sharp cusp, lacking cheek notch; coxa 1 anteroventral corner smoothly rounded, posteroventral corner notched; gnathopods 2 symmetrical; gnathopod

2 palm transverse with defining tooth projecting beyond palmar margin, palmar margin spinous with sinus midway; dactylus of peraeopods with accessory tooth; third pleonal epimeron posterior margin entire; uropod 3 rami subequal, truncate, 1.2 times as long as peduncle; telson wider than long, cleft 70%, inner margins produced to apical tooth, apices armed with 3-5 spines of varying lengths, longest spines longer than telson.

Remarks. The species within the “*quadrimana* complex” (J.L. Barnard, 1972b) of *Maera* usually show considerable variation in the palm of gnathopod 2 and this is true of *M. reishi* from the Lizard Island material. The undeveloped gnathopod has an evenly convex palm with an incision adjacent to the defining tooth, and the dactylus lacks the inner acclivity. The developed palm exhibits two forms; the deep sinus midway along the palm may be either quadrate or concave. Both forms have a strong inner dactylar acclivity and both forms are found amongst males and females. The material illustrated by J.L. Barnard (1979) showed only the concave form in the developed palm of gnathopod 2, and the sinus appears shallower.

A 3.9 mm male was found with unequal second gnathopods. The left second gnathopod was smaller

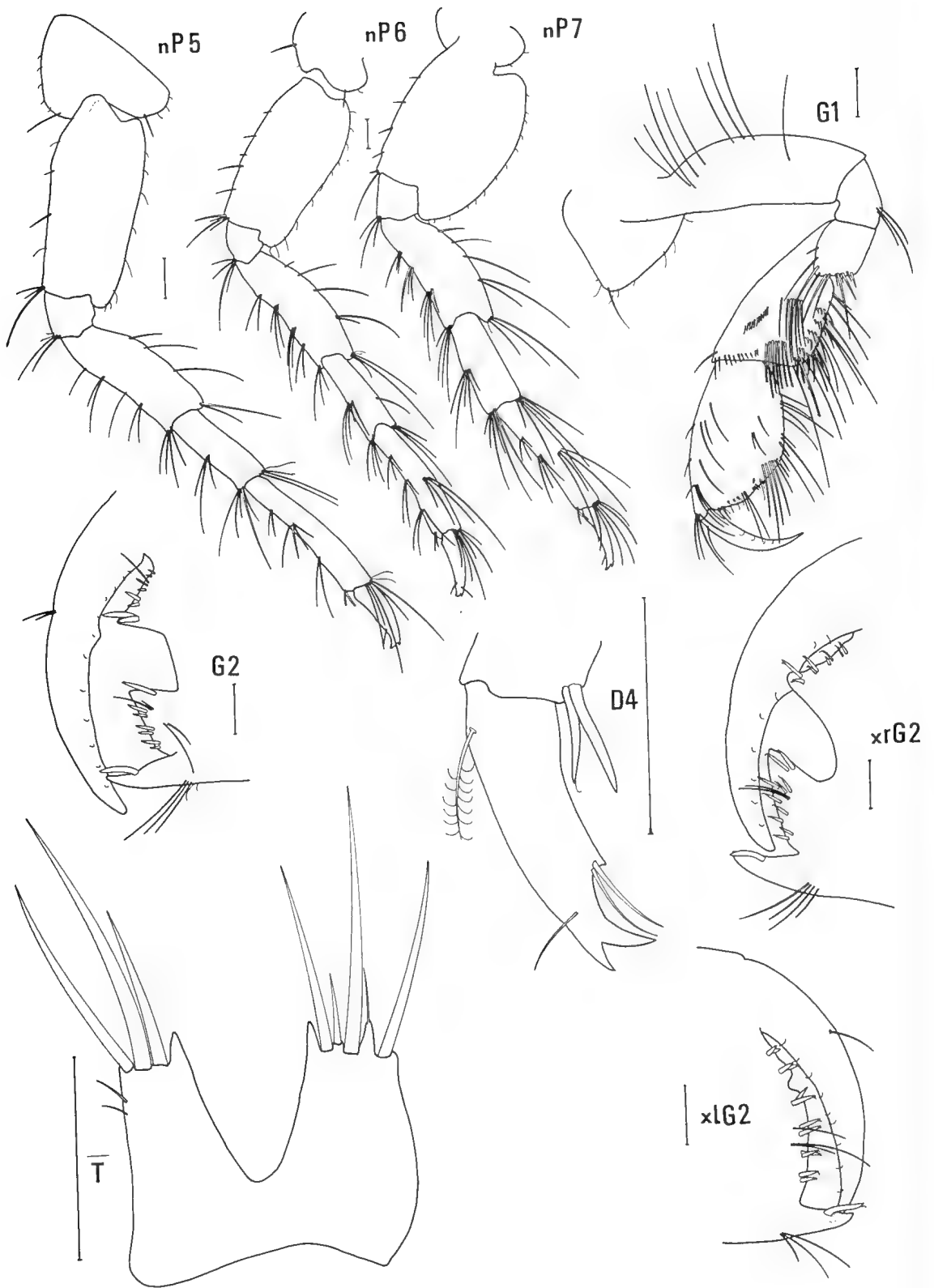


Fig. 23. *Maera reishi* Barnard, female, 4.8 mm, 76 LIZ B; n = male, 4.8 mm, 76 LIZ B; x = male, 3.9 mm, 76 LIZ B. Scale lines represent 0.1 mm.

than the right and had a poorly developed palm, suggesting that it was undergoing regeneration. The mid-sinus of the palm was small, concave and shallow, and the dactylus lacked an inner acclivity. The palm of the right gnathopod had a deep sinus of the concave form and the dactylus had a strong inner acclivity. J.L. Barnard (1970) observed a similar phenomenon in a small male *M. quadrimana* from Hawaii.

J.L. Barnard (1979) found that *M. reishi* at the northern limit of its range in California reached a length just less than 7 mm, and to the south in Mexican waters the species was less than 5 mm in length. In the material examined from Lizard Island and adjacent reefs, *M. reishi* reached 5.6 mm in length.

In the material at hand *M. reishi* has a narrow article 2 on pereopods 5 and 6 (0.4 times as wide as long), but a wider ovate article 2 on pereopod 7 (0.7 times as wide as long). This character was used to separate *M. reishi* from *M. quadrimana* for those specimens with an undeveloped palm. *Maera quadrimana* has article 2 of pereopods 5-7 narrow. Schellenberg (1938) used the differences of article 2 of pereopods 5-7 to separate *M. quadrimana* from *M. pacifica*, which has article 2 of pereopods 5-7 ovate.

Maera reishi was found in reef rock samples covered with algae including green algae *Chlorodesmis* from Lizard Island in depths to 18 metres.

Distribution. Gulf of California (type locality, Isla Espiritu Santo); Galapagos Islands; California; Lizard Island.

Maera serrata Schellenberg, 1938

Fig. 24

Maera tenella. Walker, 1904:272, pl. 5, fig. 31; Tattersall, 1922:8; Pirlet, 1936:309 (*fide* Sivaprakasam, 1966).

Maera sp.—K.H. Barnard, 1931:124.

Maera inaequipes serrata Schellenberg, 1938:41-42, fig. 18.—

J.L. Barnard, 1962:99, 1965:510; Sivaprakasam, 1966:100-101, 1968:35; Surya Rao, 1972:194.

Maera serrata.—J.L. Barnard, 1970:155-156, figs 96, 97; 1971:77, 84, figs 38, 40, 41; 1972b:107; Ledoyer, 1972:229, 231, pl. 46; 1978:279; Griffiths, 1973:286; Ortiz, 1978:8.

Material. AM P30127 to AM P30132 from the following stations: 75 LIZ 3-3 (1), 76 LIZ A (1), 87 LIZ B (3), L1-1 (8), L1-11 (1), L1-50 (1).

Diagnosis. Head with anteroventral cephalic corner produced as sharp cusp, lacking cheek notch; coxa 1

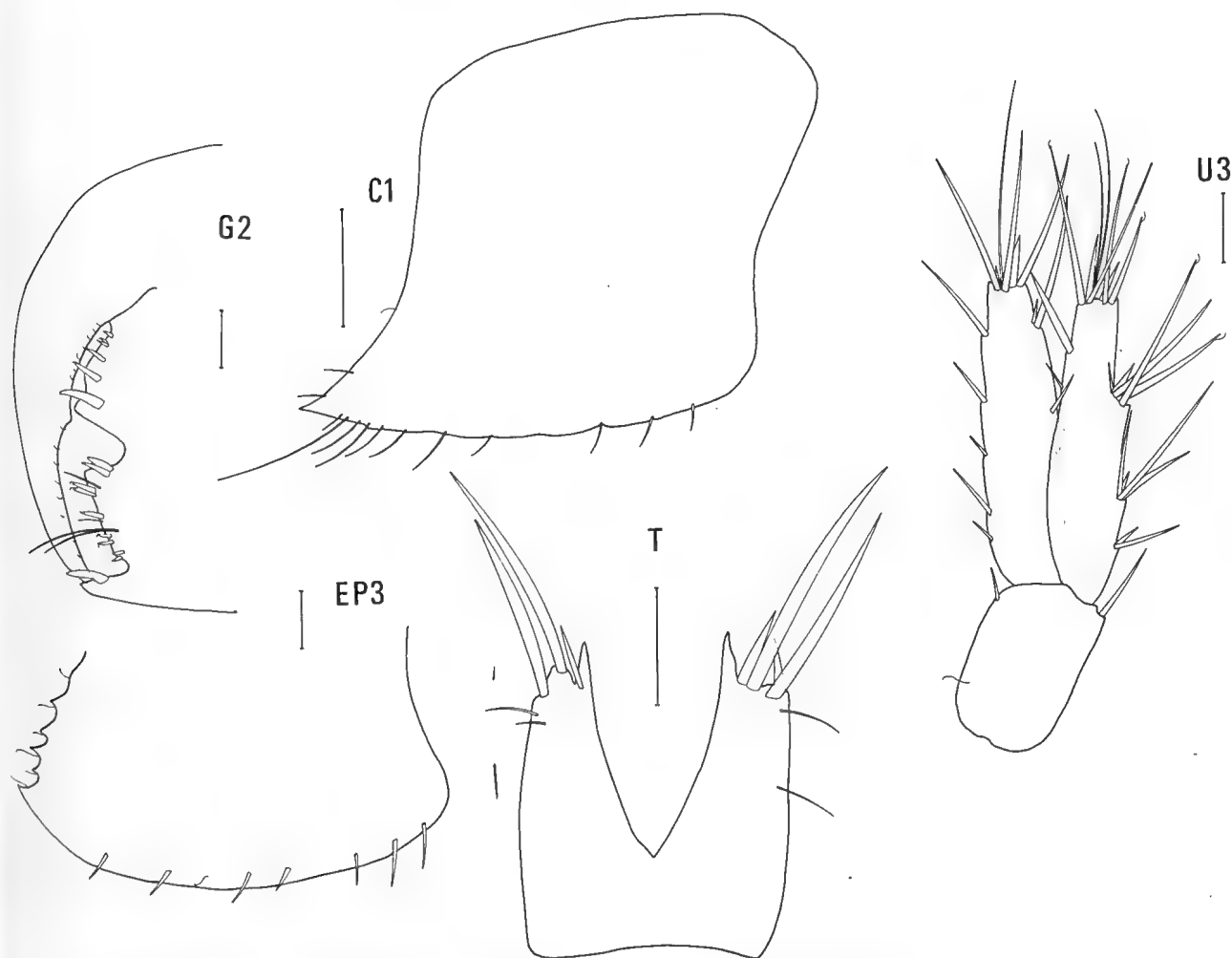


Fig. 24. *Maera serrata* Schellenberg, female, 4.8 mm, 76 LIZ A. Scale lines represent 0.1 mm.

anteroventral corner drawn to acute point, lacking posteroventral notch; gnathopods 2 symmetrical; gnathopod 2 palm transverse with defining tooth projecting beyond palmar margin, palmar margin spinous with sinus midway; dactylus of peraeopods with accessory tooth; third pleonal epimeron posterior margin serrate; uropod 3 rami equal, 1.6 times as long as peduncle; telson longer than wide, cleft 70%, inner margins produced to apical tooth, apices armed with 2-3 spines.

Remarks. The palm of gnathopod 2 in *M. serrata* may show considerable variation in its development. In the original description Schellenberg (1938) figured a 5 mm male with a rounded sinus opposite the dactylar acclivity, plus a sinus adjacent to the defining tooth. He noted that a 5 mm ovigerous female had the rounded sinus but it was slightly smaller than that of the male. J.L. Barnard (1970) figured a 5.4 mm female with an evenly convex palm lacking any sinuses. He noted that the males in his collection also had shallower sinuses in the middle of the palm than those in Schellenberg's material. Sivaprakasam (1966) found specimens up to 6 mm in length with only a small sinus in the mid-palm.

In the material I examined the palm is well developed. Females of 4.6 mm and 4.8 mm have a palm similar to that figured by Schellenberg (1938) for the male.

In the material at hand coxa 1 is more strongly produced anteriorly than shown by J.L. Barnard (1970). The posterior border of the third pleonal epimeron is more strongly serrate than that figured by Schellenberg (1938) and resembles J.L. Barnard's (1970) figure.

Maera serrata was found in reef rock, dead coral and algal samples from Lizard Island in depths to 12 metres.

Distribution. Micronesia (type locality, Gilbert Islands); Hawaii; Madagascar; Mauritius; Bay of Bengal; east coast of South Africa; Cuba; Abrolhos Islands; Lizard Island.

Genera *Mallacoota* Barnard and *Pareiasmopus* Stebbing

The genus *Pareiasmopus* erected by Stebbing (1888) includes those species with dorsal carinae on urosomite 1, with a short article 2 of the mandibular palp and the ventroposterior margin of epimeron 3 serrate.

Another flock of species with bicarinate urosomite 1 was contained within the genus *Maera*, and, in keeping with the diagnosis of that genus, has article 2 of the mandibular palp longer than article 1 and the ventral margin of epimeron 3 entire. J.L. Barnard (1972a) argued that the bicarinate "maeras" warranted generic segregation and so erected the genus *Mallacoota*, which includes *M. diemenensis* (Haswell), *M. subcarinata* (Haswell), *M. insignis* (Chevreux), *M. latibrachium* (Walker), *M. odontoplax* (Pirlot), *M. carausui* Ortiz and *M. subinsignis* Ledoyer.

A bicarinate species was found in the material from Lizard Island and adjacent reefs that would not be placed in either *Mallacoota* or *Pareiasmopus* as defined by Barnard and Stebbing. The species has article 2 of the mandibular palp shorter than article 1, and the

ventral margin of the third pleonal epimeron entire. It is here placed in *Mallacoota* (*M. balara* n.sp.) because the mandibular palp is of the *Mallacoota* form despite the fact that article 2 is shorter than article 1. The 3-articulate mandibular palp in *Mallacoota* has a form which is distinct from that of *Pareiasmopus*.

The *Pareiasmopus* palp is described as follows: article 1 curves around the upper lip, widens distally, and is longer than article 2; article 2 is geniculate; article 3 is linear and does not have a medial comb row of setae.

The *Mallacoota* palp has article 1 linear and not curved around the upper lip; article 2 is not geniculate; article 3 is linear and does not have a medial comb row of setae. J.L. Barnard's (1972a) original diagnosis of the genus *Mallacoota* stated "article 2 never shorter than 1 but article 1 occasionally as long as article 2". However, because *Mallacoota balara* has a palp of the *Mallacoota* form, and has the ventral margin of epimeron 3 entire, it is proposed that the diagnosis of the mandibular palp for the genus should be: article 2 may be shorter, equal to, or longer than article 1.

Although the genus *Mallacoota* was erected for the bicarinate maeras, J.L. Barnard's diagnosis for the genus allowed the mandibular palp to be either absent, 1-articulate, or 3-articulate. Lowry and Fenwick (1983) are erecting a new genus to include the species of *Mallacoota* that have a 1-articulate mandibular palp.

The species of *Mallacoota* recorded from Australia are *M. diemenensis* and *M. subcarinata* from south-eastern Australia (J.L. Barnard, 1972a) and *M. balara* n.sp. from the Lizard Island material.

Sheard (1937) listed *Pareiasmopus suluensis* (Dana) as the only species of *Pareiasmopus* recorded in Australia. Stebbing (1888) recorded *P. suluensis* from Torres Strait near Cape York (10°30'S, 142°18'E) and Chilton (1922) recorded *P. suluensis* from north-western Australia. Stebbing (1888), however, stated that his species had dorsal teeth on peraeonite 7, and therefore incorrectly attributed it to *P. suluensis*. Chilton (1922) made the same error, so there is no valid record of *P. suluensis* from Australia.

J.L. Barnard (1972a) recorded three species of *Pareiasmopus* from Australia: *P. setiger* Chevreux from Torres Strait, *P. echo* Barnard from off Bunbury and *P. ya* Barnard from Cockburn Sound. *Pareiasmopus setiger* was described by Chevreux (1901) from the Seychelle Islands and Barnard (1972a) synonymized *Megamoera suensis* Haswell, 1880b with *P. setiger*. Barnard used the junior synonym because he regarded Haswell's original description as "too sparse for positive identification". *Megamoera suensis* was described from the Sue Islands in Torres Strait.

Later, J.L. Barnard (1974) reported differences between *P. setiger* and *P. suensis* and so revived Haswell's species. An examination of Chevreux's type material confirmed that *P. setiger* differs from *P. suensis*.

The material from Lizard Island and adjacent reefs included *P. echo* Barnard and *P. suensis* (Haswell). This

is the first record of *P. echo* from the east coast of Australia.

Mallacoota balara n.sp.

Figs 25, 26

Type material. HOLOTYPE, male, 6.4 mm, AM P30133; ALLOTYPE, 6.8 mm, AM P30134; 2 PARATYPES AM P30135; fringing reef, between Bird Islet and South Island, Lizard Island (14°42'S, 145°28'E), from reef rock, 12 m depth, P.A. Hutchings, 1 August 1977, 76 LIZ A; 1 PARATYPE, male, AM P30136, reef back, Yonge Reef (14°36'S, 145°37'E), from dead *Acropora*, 5 m depth, P.B. Berents and P.A. Hutchings, 7 January 1975, 75 LIZ C-1; 4 PARATYPES, AM P30137; 1 PARATYPE, USNM 190701, off Mangrove Beach, Lizard Island (14°41'S, 145°27.6'E) from mixed algae, 2 m depth, J.K. Lowry, 28 September 1978, LI-1; 2 PARATYPES, AM P30138, type locality, P.A. Hutchings, 6 November 1976, 76 LIZ A; 1 PARATYPE, USNM 190700, off Chinaman's Head, Watson's Bay, Lizard Island (14°40'S, 145°27'E), from reef rock, 7 m depth, P.A. Hutchings, 7 November 1976, 76 LIZ B.

Additional material. AM P30139 to AM P30153 from the following stations: 75 LIZ 5-1 (1), 75 LIZ 7-3 (1), 75 LIZ 13-2 (2), 75 LIZ C-1 (2), 75 LIZ 0-3 (1), 75 LIZ S-2 (5), 76 LIZ A(36), 76 LIZ B(24), 76 LIZ 16(5), LI-1(9), LI-16(1), LI-48 (4), LI-50 (5), LI-61 (10), LI-62 (9).

Diagnosis. Article 2 of mandibular palp 0.8 times as long as article 1; coxae 1-4 with ventral margin notched posteriorly; article 2 of male gnathopod 2 wide; article 6 of male gnathopod 2 with oblique palm defined by cusp bearing setae, palmar margin with proximal and distal shallow sinuses; pleonites 1-3 lack dorsal teeth; posteroventral corner third pleonal epimeron produced to form a cusp, posterior and ventral margins entire; outer and inner rami of uropod 3 equal, 1.2 times as long as peduncle; telson cleft midway, notched apices bearing 3 spines.

Description. Holotype male, 6.4 mm. *Head* as long as first two pereonites, anteroventral corner notched, eye almost filling lobe, dark brown in alcohol. *Antenna 1* twice as long as antenna 2; article 1 with distal spine, article 2 subequal to article 1, article 3, 0.3 times as long as article 1; flagellum 1.5 times as long as peduncle, 21-articulate; accessory flagellum 3-articulate, article 3 small, almost extending to end of article 2 of primary flagellum. *Antenna 2* peduncle longer than flagellum, article 3 longest; flagellum 8-articulate.

Mandible with incisor and 4 accessory blades; lacinia mobilis with 5 teeth; molar triturating; mandibular palp 3-articulate, article 2, 0.8 times as long as article 1, article 3 equal to article 1. *Maxilla 1*: inner plate with 2 plumose apical setae and fine marginal setae; outer plate armed with 3 bifid and 4 serrate spine teeth; palp 2-articulate, article 2 with apical and distal inner marginal setae. *Maxilla 2*: inner and outer plates with distal setae. *Maxillipeds*: inner plate with fine plumose apical and inner marginal setae; outer plate with stout plumose apical setae; palp 4-articulate, articles 2 and 3 sparsely setose.

Gnathopod 1: coxa 1.3 times as long as wide, posteroventral notch bearing seta, ventral margin

sparsely setose; article 5, posterior margin densely setose, two medial groups of setae; article 6 equal to article 5, tufts of setae spaced along posterior margin, medial comb row of setae, oblique palm defined by stout spine, palmar margin bearing setae and small spines; dactylus slender, extends beyond palm. *Gnathopod 2* stouter, more robust than gnathopod 1; coxa 1.3 times as long as wide, posteroventral notch bearing seta, ventral margin sparsely setose; article 2 wide, 0.5 times as wide as long; article 3 bearing two prominent carinae on dorsal surface; article 5 compressed, stout anteroventral spine, smaller proximal spine, posterior margin densely setose, some pectinate setae; article 6, 1.8 times as long as wide with 5 superior medial spines, posterior margin bearing tufts of setae, oblique palm defined by cusp bearing setae, palmar margin with proximal and distal shallow sinuses, protrusion bearing spine and setae separating sinuses, distal palmar margin bearing 3 stout spines and setae; dactylus extending beyond defining cusp.

Peraeopod 3: coxa 1.5 times as long as wide, posteroventral corner notched, ventral margin sparsely setose; article 4 widening distally, anterior margin with 2 spines, posterior margin sparsely setose; article 5 subequal to article 4, posterior margin spinous; article 6, 1.4 times as long as article 5, posterior margin spinous, distal pair of striate locking spines; dactylus apically constricted, bearing a seta and setule at constriction, a seta and plumose seta on anterior margin. *Peraeopod 4*: very similar in size and proportion to peraeopod 3 except coxa not posteroventrally notched but posteriorly produced. *Peraeopod 5*: coxa bilobed ventrally, 0.7 times as wide as long; article 2 ovate, 0.8 times as wide as long, distal anterior margin spinous, posterior margin sparsely setose; article 4, posterior and anterior margins extended ventrally, margins spinous; article 5, 0.8 times as long as article 4; article 6, 1.5 times as long as article 4, anterior margin spinous, posteroventral corner bearing spines and setae; dactylus stout, apically constricted, bearing seta and setules at apical constriction. *Peraeopod 6* similar to peraeopod 5 but longer, stouter and more setose; coxa not bilobed ventrally; articles 4, 5 and 6 wider. *Peraeopod 7* same size and proportions as peraeopod 6.

Third pleonal epimeron: posteroventral corner produced to form a cusp, posterior and ventral margins entire, ventral margin bearing 3 spines.

Urosomite 1 dorsally bicarinate. *Uropod 3*: distal margin of peduncle spinous; outer ramus 1.2 times as long as peduncle with apical spines, spines along inner and outer margins; inner ramus equal to outer ramus, apical spines and a seta, outer margins spinous. *Telson* cleft midway, apices notched, bearing 3 spines.

Allotype female, 6.8 mm. Similar to male except in following ways: *Gnathopod 2* more slender; coxa 1.7 times longer than wide; article 2 not broad, 0.3 times as wide as long; article 5 not compressed, 0.8 times as long as article 6, spines on anterior margin absent; article 6, 2.2 times as long as wide with superior and inferior medial setae, oblique palm defined by two

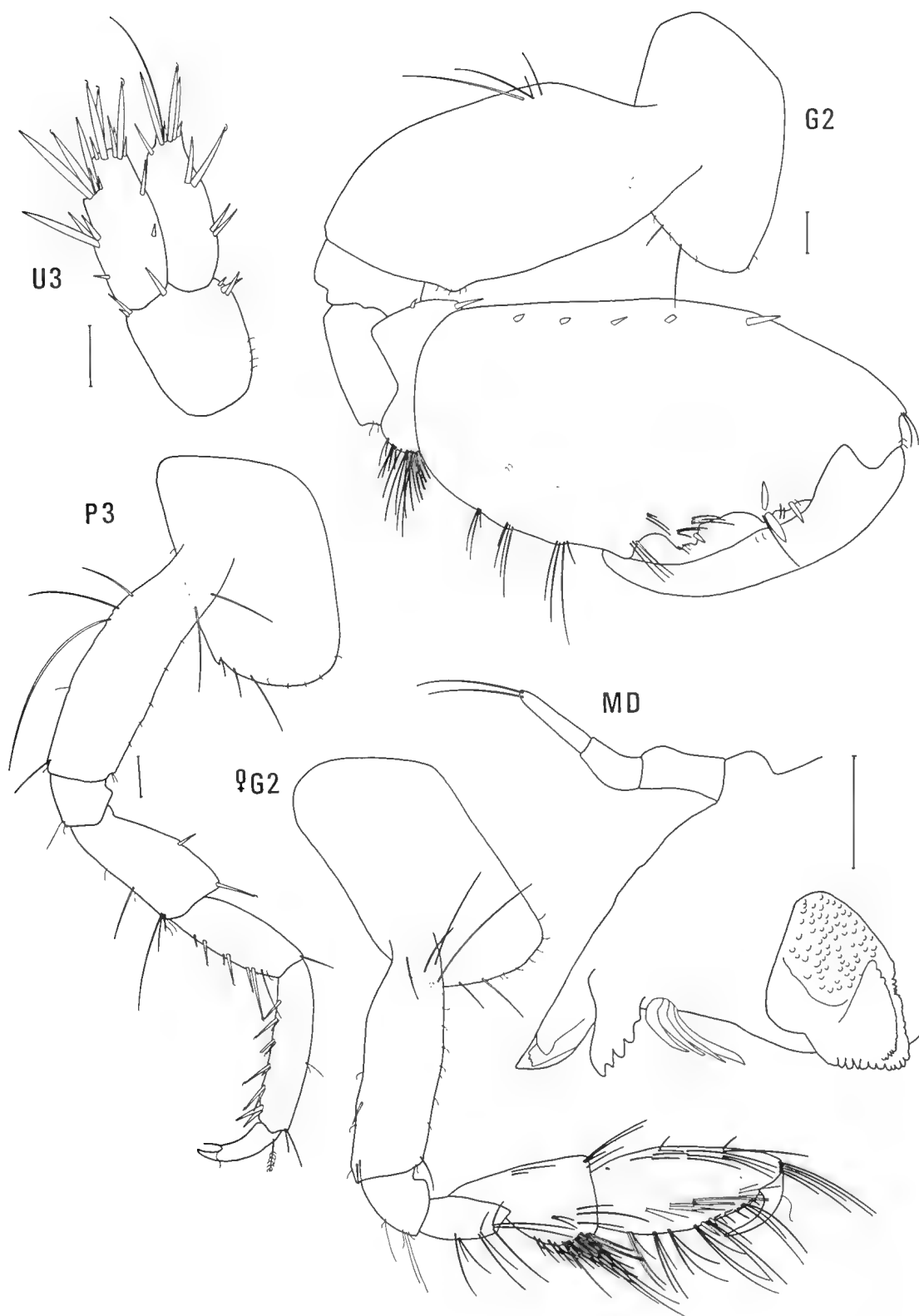


Fig. 25. *Mallacoota balara* n.sp., holotype, male, 6.4 mm, 76 LIZ A; female = allotype, 6.8 mm, 76 LIZ A. Scale lines represent 0.1 mm.

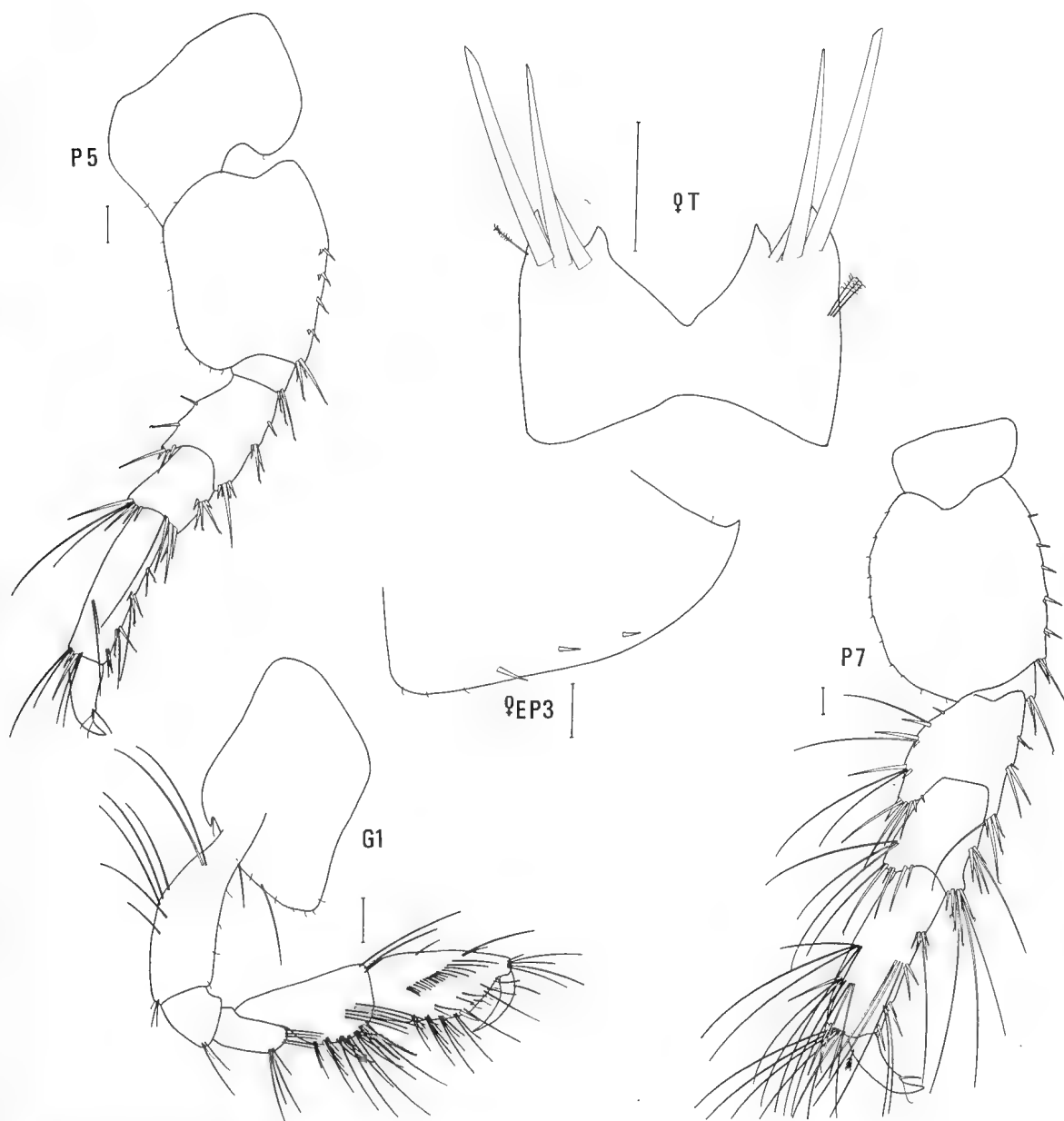


Fig. 26. *Mallacoota balara* n.sp., holotype, male, 6.4 mm, 76 LIZ A; female = allotype, 6.8 mm, 76 LIZ A. Scale lines represent 0.1 mm.

unequal spines, palm lacks sinuses, bears short setae; dactylus slender, reaches defining spines. *Peraeopods* 6 and 7: similar size to male except more slender and less setose.

Variation. The number of articles in the accessory flagellum of antenna 1 is constant, but the accessory flagellum varies in length relative to the primary flagellum, from as long as first article of the primary flagellum to as long as the first three articles of the primary flagellum. The palm of gnathopod 2 of smaller males has shallower sinuses. *Peraeopods* 6 and 7 of males greater than 4.9 mm in length are much more setose than in smaller males. Some specimens have a terminal seta from both outer and inner rami of uropod

3 suggesting that this may be broken in the holotype. Article 2 of the mandibular palp varies from 0.6 times as long as article 1, to 0.8 times as long as article 1.

Remarks. The specific epithet *balara* is the name of one of the Aboriginal tribes in the Cape Flattery area.

Mallacoota balara is closely related to *Mallacoota latibrachium* (Walker), described from the Maldives and Laccadive Archipelagoes. The mandibular palp of *M. latibrachium* has article 1 "scarcely shorter than" article 2 (Walker, 1906). Both *M. latibrachium* and *M. balara* have poorly setose male second gnathopods. The male second gnathopod of *M. latibrachium* has a wide article 2 as seen in *M. balara*, but article 6 has small tubercles over the distal surface. The palm is oblique but lacks

sinuses. Walker's description (1906) of peraeopods 5-7 of a 5 mm specimen, suggests that they are less setose than peraeopods 5-7 of *M. balara*. The uropods of both species have subequal rami longer than the peduncle. The telson of *M. latibrachium* is cleft to the base but *M. balara* has the telson cleft midway.

Mallacoota balara was found in dead coral *Acropora* and reef rock covered with coralline algae

Lithothamnion from the reef back at Yonge Reef in depths from 2 to 5 metres. At Lizard Island *M. balara* was found in dead coral *Acropora* and reef rock covered with coralline algae *Lithothamnion* and green algae *Chlorodesmis*, in samples of brown algae *Dictyota* and coral rubble from subtidal to 15 metres.

Distribution. Lizard Island (type locality); Yonge Reef.

Key to the Genus *Mallacoota*

1. Posterior margin of pleonites 1-3 bearing 2 mid-dorsal teeth 2
 — Posterior margin of pleonites 1-3 dorsally smooth 3
2. Article 6 of male second gnathopod densely setose; article 2 of peraeopod 7 has posterior margin crenulate *M. diemenensis* (Haswell, 1880a)
 — Article 6 of male second gnathopod poorly setose; article 2 of peraeopod 7 has posterior margin smooth *M. carausui* Ortiz, 1976
3. Article 6 of male second gnathopod densely setose 4
 — Article 6 of male second gnathopod poorly setose 5
4. Articles 4 and 5 of male peraeopods 6 and 7 wider than long; palm of gnathopod 2 not distinct *M. insignis* (Chevreux, 1901)
 — Articles 4 and 5 of male peraeopods 6 and 7 longer than wide; palm of gnathopod 2 distinct *M. subcarinata* (Haswell, 1880a)
5. Articles 4 and 5 of male peraeopods 6 and 7 wider than long
 *M. subinsignis* Ledoyer, 1979
 — Articles 4 and 5 of male peraeopods 6 and 7 longer than wide 6
6. Male second gnathopods medial face with small tubercles increasing in size distally *M. latibrachium* (Walker, 1906)
 — Male second gnathopods medial face without small tubercles 7
7. Male second gnathopods medial face shallowly excavate
 *M. odontoplax* (Pirlot, 1936)
 — Male second gnathopods medial face not shallowly excavate, palmar margin with 2 shallow sinuses *M. balara* n.sp.

Parelasmopus echo Barnard, 1972

Fig. 27

Parelasmopus echo J.L. Barnard, 1972a:242, 255-258, figs 148, 149.

Material. AM P30154 to AM 30158 from the following stations: 76 LIZ B (1), LI-28 (2), LI-30 (1), LI-50 (4), LI-52 (2).

Diagnosis. Article 2 of peraeopods 5-7 with acute posteroventral lobe, posterior margin deeply serrate; pleonite 3 posterior margin with 2 weak dorsal teeth.

Remarks. J.L. Barnard (1972a) described *P. echo* from 3 specimens collected in south-western Australia. The material at hand shows some variation from that described by J.L. Barnard (1972a).

The greatest variation is seen in coxae 1-4. The original description states "coxa 1 extended forward

weakly and ending in a sharp point, coxae 2-4 also with small anteroventral point, posteroventral corners of coxae 1-4 weakly serrate". In the material at hand both males (size range 4.8 mm – 10.5 mm) and females 4.3 mm – 5.6 mm) were examined and the following variation noted. Coxa 1 was found to have an anteroventral point and a strongly serrate posteroventral corner. The anteroventral corner of coxae 2-4 ranged from smoothly rounded to pointed. The posteroventral corner of coxa 2 ranged from smooth to strongly serrate. The posteroventral corner of coxae 3 and 4 ranged from notched to serrate.

The palm of the male second gnathopod also showed some variation from that in the original description. The palm of a 4.8 mm male is very similar to that shown by J.L. Barnard (1972a) for a 14.0 mm male. However, the palm of a 10.5 mm male in the material examined

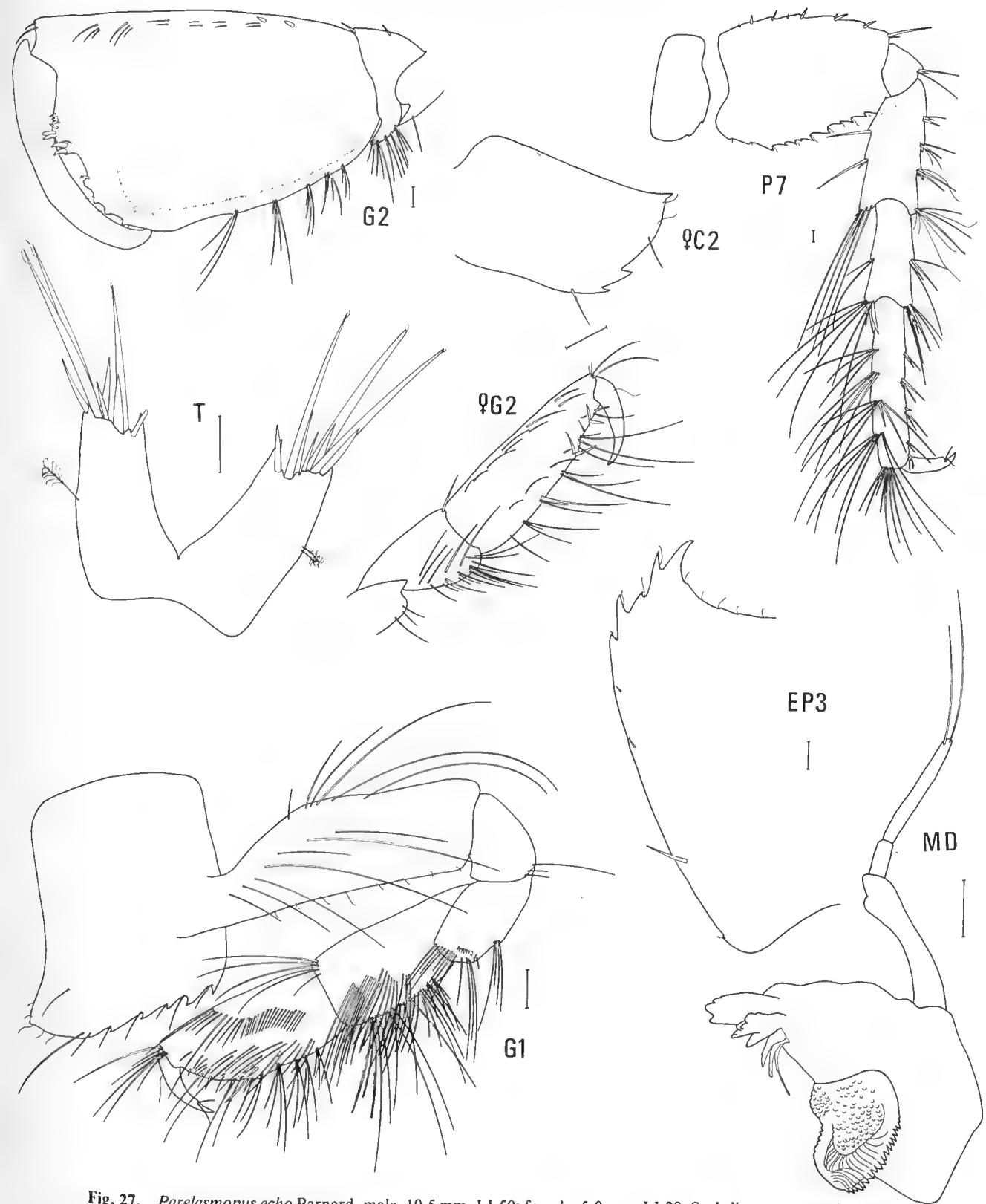


Fig. 27. *Parelasmopus echo* Barnard, male, 10.5 mm, LI-50; female, 5.0 mm, LI-28. Scale lines represent 0.1 mm.

is not strongly oblique and has a quadrate sinus in the middle rather than a "long shallow hollow" (J.L. Barnard, 1972a).

Parelasmopus echo was found in the seagrass

Halophila, algae, including coralline *Halimeda*, sediment and reef rock samples from Lizard Island.

Distribution. South-western Australia (type locality, 11 kilometres SW of Bunbury); Lizard Island.

Pareiasmopus suensis (Haswell, 1880b)

Figs 28, 29

Megamoera suensis Haswell, 1880b:335-336, pl. 21, fig. 5.
Pareiasmopus suensis.—J.L. Barnard, 1974:143.

Type material. When Haswell described *Megamoera suensis* from Sue Island in Torres Strait he did not designate a holotype and he did not state the number of specimens examine. One specimen of *Megamoera suensis* from Haswell's material is now lodged in the Australian Museum and mounted on 7 microscope slides (AM P18499). The specimen is from the Sue Island collection examined by Haswell and is one of the type series. In order to stabilize the name *Pareiasmopus suensis*, the specimen (AM P18499) is herein described and established as a lectotype.

Additional material. AM P30208 to AM P30211 from the following stations: 75 LIZ E-1 (1), 75 LIX F-1 (1), 75 LIZ N-1 (1) and 78 LIZ-PBW-9 (1).

Diagnosis. Article 2 of pereopods 5-7 with obtuse posteroventral lobe, posterior margin weakly serrate; pleonite 3 posterior dorsal margin smooth.

Description. Lectotype male. *Antenna 1*: article 1 of peduncle with 4 ventral spines; accessory flagellum 4-articulate, article 4 small, extending halfway along article 3 of primary flagellum.

Mandible with incisor and 4 accessory blades; lacinia mobilis with 4 teeth; molar triturating. *Maxilla 1*: inner plate with 2 plumose apical setae and fine marginal setae; outer plate armed with 7 spine teeth; palp 2-articulate, distally setose. *Maxilla 2*: inner and outer plates with distal setae.

Gnathopod 1: coxa 0.8 times as wide as long, anteroventral corner slightly produced with subacute point, ventral margin notched; article 4 posteroventral corner subacute; article 5, anterior margin 2.7 times as long as ventral margin, anteroventral corner setose, posterior margin setose, ventral margin with submarginal setae extending across article 6; article 6 elongate with medial comb row of setae. *Gnathopod 2*: larger, more robust than gnathopod 1, coxa with subacute anteroventral corner, ventral margin notched posteriorly; article 4 produced ventrally to sharp point;

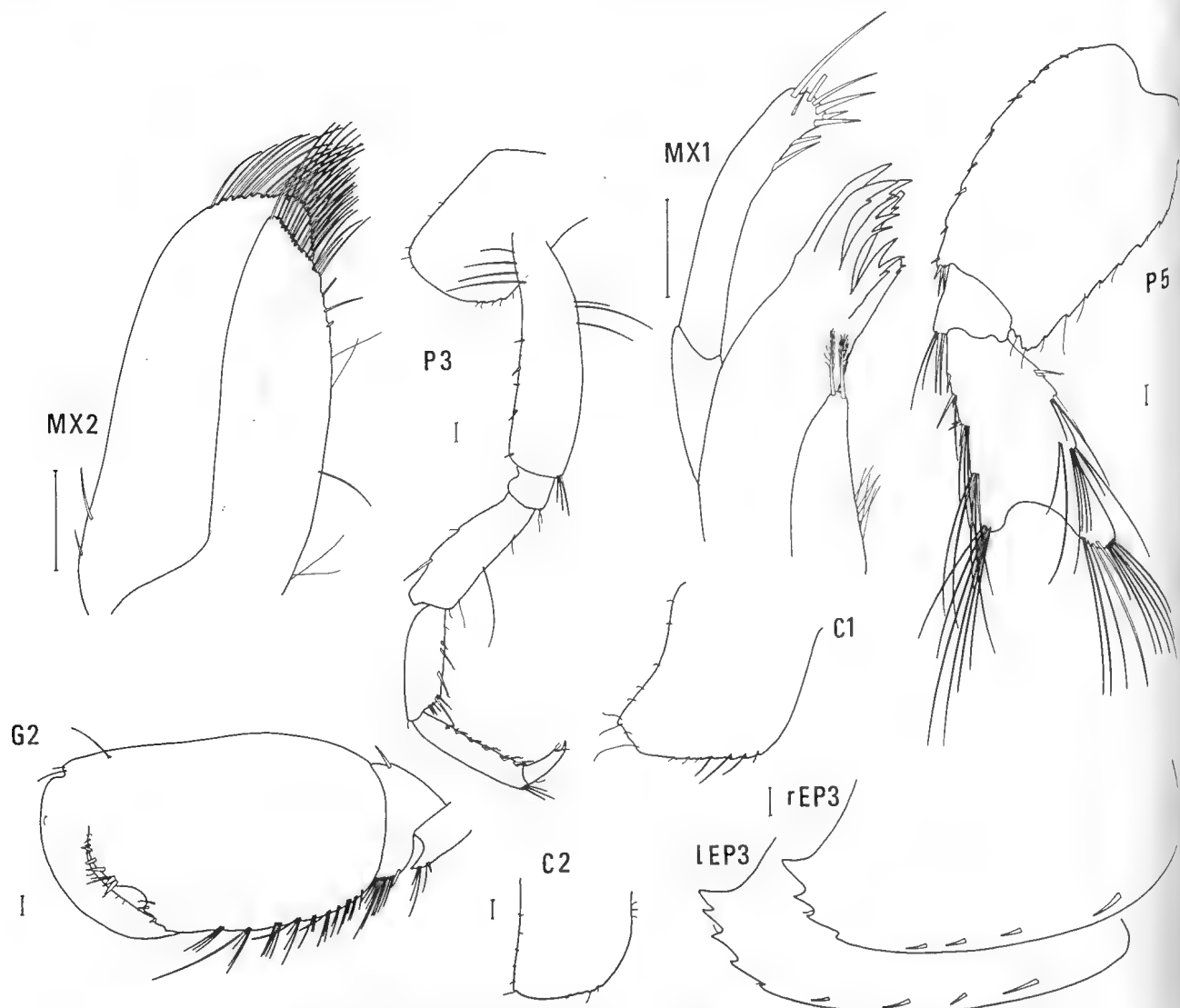


Fig. 28. *Pareiasmopus suensis* (Haswell), lectotype, male, Sue Island, Torres Strait. Scale lines represent 0.1 mm.

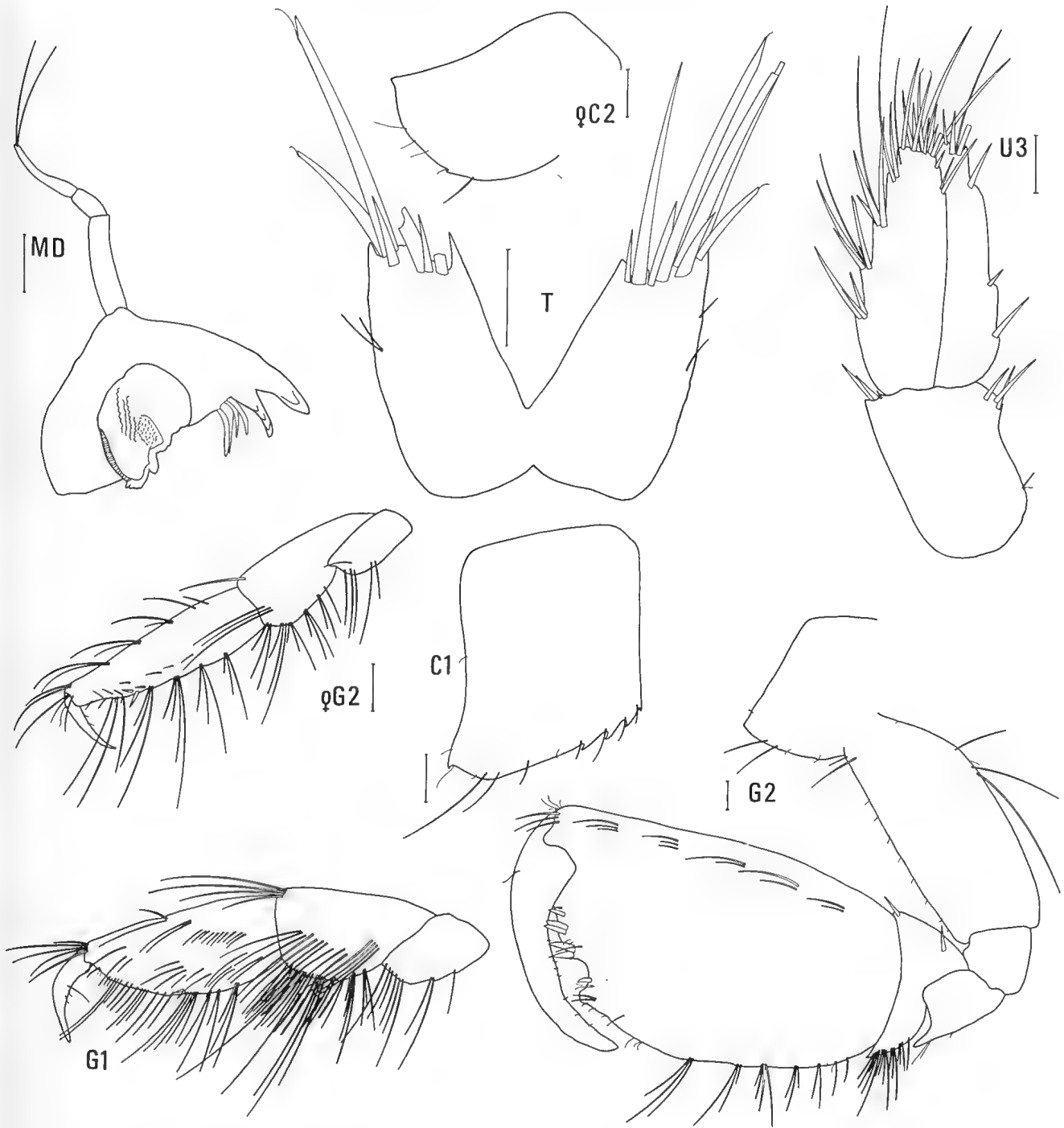


Fig. 29. *Parelasmopus suensis* (Haswell), male, 6.8 mm, 75 LIZ F-1; female, 5.6 mm, 75 LIZ E-1. Scale lines represent 0.1 mm.

article 5 compressed, anterior margin with stout spine, posterior margin densely setose; article 6 stout, posterior margin with tufts of setae, palm oblique with mid-palmar sinus, palmar margin spinous; dactylus inner margin sparsely setose.

Peraeopod 3: coxa with anteroventral corner rounded, posteroventral corner weakly notched; article 4 anteroventral corner broadly expanded; articles 5 and 6 posterior margin spinous; dactylus apically constricted with 3 setules at constriction. *Peraeopod 4*: very similar

size and proportions to peraeopod 3 except coxa 4 wider than coxa 3. *Peraeopod 5*: article 2 anterior margin spinous, posterior margin weakly serrate and sparsely setose; article 4 anterior and posterior margins setose and spinous.

Right third pleonal epimeron: ventral margin with 4 spines, posteriorly serrate with 4 teeth. *Left third pleonal epimeron*: ventral margin with 4 spines, posteriorly serrate with 5 teeth.

Male, 6.8 mm. *Head* not quite as long as first two peraeonites, cheek notch slightly gaping, anteroventral corner sharply pointed, almost reaching tangent to ocular lobe. *Antenna 1*: flagellum longer than peduncle, peduncular article 1 bearing 2 ventral spines; accessory flagellum 3-articulate, article 3 small, extending halfway along article 3 of primary flagellum. *Antenna 2*: peduncle longer than flagellum; flagellum 9-articulate.

Mandible: palp 3-articulate, article 2, 0.4 times as long as article 1, article 3, 0.8 times as long as article 1, with 2 apical setae. *Maxillipeds*: inner plate with plumose apical setae; outer plate with apical spine teeth and marginal setae; palp 4-articulate, article 2 inner margin setose.

Gnathopod 1: ventral margin of coxa posteriorly serrate; article 4 posteroventral corner smoothly rounded; article 6 elongate, tapering distally, anteroventral corner setose, posterior margin setose, medial comb row of setae and other setae on medial face, oblique palm defined by pair of spines, confluent with posterior margin, palm setose; dactylus slender, curved. *Gnathopod 2*: anterior margin article 5 with 2 stout spines.

Peraeopod 5: less setose than lectotype; coxa wider than long, anterior half longer and smoothly rounded ventrally, posteroventral corner notched; article 4 anterior margin setose, posterior margin with 2 spines, posteroventral corner spinous and setose; article 6 anterior margin armed with groups of spines and long setae, posterior margin bearing groups of long setae, posteroventral corner with spines and setae; dactylus apically constricted with slight protrusion marking the constriction, a seta and setule at constriction. *Peraeonite 7* posterior margin with a pair of mid-dorsal teeth. *Peraeopod 7*: coxa, articles 5, 6 and dactylus missing; articles 2, 3 and 4 similar proportions to peraeopod 5 but larger.

Pleonites 1 and 2: posterior margin with 2 mid-dorsal teeth. *Pleonite 3*: posterior margin dorsally smooth. *Third pleonal epimeron*: ventral margin with 3 spines, posteriorly serrate with 4 teeth.

Urosomite 1 dorsally bicarinate. *Uropod 3*: distal margin peduncle spinous; outer ramus 1.4 times as long as peduncle, apically spinous, outer margin with groups of spines and setae; inner ramus equal to outer ramus, apically spinous, 3 spines spaced along inner margin. *Telson* cleft 77%, apices blunt, with inner and outer margins extended sharply, 6-8 apical spines with longest spines longer than telson.

Female, 5.6 mm. Similar to male except in following ways: *Gnathopod 1*: article 5 less setose; article 6 with fewer medial setae, palm defined by 3 spines. *Gnathopod 2*: coxa with stronger anteroventral tooth, stronger notch in ventral margin; article 4 posteroventral corner rounded, not produced; article 5 not compressed, dorsal margin twice as long as ventral margin; article 6 elongate, 3.5 times as long as wide, tapering distally, palm confluent with posterior margin defined by a stout

spine; dactylus slender. *Peraeopods 3 and 4*: articles 5 and 6 less spinous. *Peraeopod 5* less setose.

Remarks. *Pareiasmopus suensis* was found in reef rock and coral rubble at Yonge Reef in depths from 12 to 30 metres. Some samples of reef rock and coral rubble were covered with *Halimeda* and other coralline algae and others were devoid of algae.

Distribution. Sue Island, Torres Strait (type locality); Yonge Reef.

DISCUSSION

The Melitidae of the northern Barrier Reef are quite distinct from those of south-eastern Australia. Studies have not been published concerning the Melitidae from the southern portion of the Great Barrier Reef. The few published records of melitids from the east coast do not include any of the species from Lizard Island and adjacent reefs and therefore do not give any indication of the southern limits of the northern Barrier Reef fauna. Two species from south-western Australia were found in the Lizard Island area: *Pareiasmopus echo* and *Maera serrata*. *Maera serrata* has a wide distribution in the tropical and subtropical Indo-Pacific but *P. echo* was previously known only from south-western Australia. J.L. Barnard (1972a) did not record either of these species from southern Australia; this suggests that their distribution is around the north-western coastline to the Great Barrier Reef.

All species in the genus *Elasmopus* were found associated with algae and reef rock except *E. spinicarpus*, which occurred only in one sample taken from under stones at low tide. *Ceradocus oxyodus* and *C. woorree* were found with *E. spinicarpus*. The only Melitidae found in sediment were *C. woorree*, *Maera octodens* and *M. griffini*. The other species of *Maera*, *Pareiasmopus*, *Mallacoota balara*, *Dulichella appendiculata* and *Ceradocus yandala* occurred in samples from reef rock, algae and seagrasses.

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Appendix A: Station List

75 LIZ 1-2	Off Station Beach, Lizard Island, 6
75 LIZ 1-5	January 1975, P.B. Berents and P.A. Hutchings, dead <i>Pocillopora</i> , 3 metres.
75 LIZ 3-3	Off Crystal Beach, Lizard Island, 14 January 1975, P.B. Berents and P.A. Hutchings, reef rock encrusted with sponge, <i>Lithothamnion</i> and brown algae, 11 metres.
75 LIZ 4-3	Off Crystal Beach, Lizard Island, 15 January 1975, P.B. Berents and P.A. Hutchings, reef rock encrusted with brown algae and alcyonarians, 18 metres.
75 LIZ 5-1	Off Crystal Beach, Lizard Island 15 January 1975, P.B. Berents and P.A. Hutchings, dead <i>Acropora</i> heavily encrusted with <i>Lithothamnion</i> and brown algae, 9 metres.
75 LIZ 7-3	Off Coconut Beach, Lizard Island, 17 January 1975, P.B. Berents and P.A. Hutchings, reef rock encrusted with algae, 15 metres.
75 LIZ 13-2	Off NE face Lizard Island, 6 January 1975, P.B. Berents and P.A. Hutchings, dead <i>Acropora</i> , 1 metre.
75 LIZ C-1	Reef back, Yonge Reef, 7 January 1975, P.B. Berents and P.A. Hutchings, flat plates of dead <i>Acropora</i> from bommie, P.B. Berents and P.A. Hutchings, 5 metres.
75 LIZ D-1	Outer slope, Yonge Reef, 9 January 1975, P.B. Berents and P.A. Hutchings, reef rock with <i>Halimeda</i> and <i>Lithothamnion</i> , 36 metres.
75 LIZ E-1	Outer slope, Yonge Reef, 9 January 1975, P.B. Berents and P.A. Hutchings, reef rock with <i>Halimeda</i> and <i>Lithothamnion</i> , 30 metres.

75 LIZ F-1	Outer slope, Yonge Reef, 9 January 1975, P.B. Berents and P.A. Hutchings, coral rubble covered with <i>Halimeda</i> and other algae, 18 metres.	LI-21	Fringing reef, between Bird Islet and South Island, Lizard Island, 7 October 1978, J.K. Lowry, <i>Halophila</i> , mixed algae, <i>Caulerpa</i> , <i>Halimeda</i> sample with coral rubble, predominated by platelet forams, 24-28 metres.
75 LIZ N-1	Outer slope, Yonge Reef, 12 January 1975, P.B. Berents and P.A. Hutchings, reef rock with <i>Halimeda</i> from outside a cave, 24 metres.	LI-27	Fringing reef, between Bird Islet and South Island, Lizard Island, 9 October 1978, J.K. Lowry, <i>Halophila</i> , mixed algae and sediment from grassbeds off reef base, 24 metres.
75 LIZ O-3	Reef back, Yonge Reef, 13 January 1975, P.B. Berents and P.A. Hutchings, reef rock with green algae, 3 metres.		
75 LIZ S-2	Reef back, Yonge Reef, 19 January 1975, P.B. Berents and P.A. Hutchings, dead <i>Acropora</i> , heavily encrusted with <i>Lithothamnion</i> , 2 metres.	LI-28	Fringing reef, between Bird Islet and South Island, Lizard Island, 9 October 1978, P.C. Terrill, <i>Halophila</i> , mixed algae and sediment from grassbeds off reef base, 24 metres.
75 LIZ T-1	Reef back, Yonge Reef, 19 January 1975, P.B. Berents and P.A. Hutchings, dead <i>Acropora</i> , 2 metres.	LI-30	Fringing reef, between Bird Islet and South Island, Lizard Island, 9 October 1978, P.C. Terrill, <i>Halophila</i> and mixed algae from grassbeds off reef base, 24 metres.
75 LIZ V-3	Reef back, Yonge Reef, 20 January 1975, P.B. Berents and P.A. Hutchings, reef rock cemented with <i>Lithothamnion</i> and some <i>Halimeda</i> from bommie, 2 metres.	LI-37	Eastern end, Mangrove Beach, Lizard Island, 10 October 1978, A.R. Jones, core sample positioned over body burrow in sand bottom, 1.5 metres.
76 LIZ 16	Off western side of Palfrey Island, Lizard Island, 12 January 1976, P.B. Berents and P.A. Hutchings, washing from reef rock, 6 metres.	LI-39	Casuarina Beach, Lizard Island, 11 October 1978, J.K. Lowry, A.R. Jones and P.C. Terrill, under stones at low tide mark.
76 LIZ A	Fringing reef, between Bird Islet and South Island, Lizard Island, April, July, November 1976, January, April, July, November 1977, January 1978, P.B. Berents and P.A. Hutchings, reef rock, 12 metres.	LI-48	Mermaid Cove, Lizard Island, 14 October 1978, J.K. Lowry, mixed algae, <i>Dictyota</i> and a filamentous green <i>Chlorodesmis</i> , coral rubble and silt, subtidal to 2 metres.
76 LIZ B	Off Chinaman's Head, Lizard Island, April, July, November 1976, January, April, July, November 1977, January 1978, P.B. Berents and P.A. Hutchings, reef rock, 7 metres.	LI-49	Off North Point, Lizard Island, 14 October 1978, J.K. Lowry, red algae and coral rubble from subtidal caves, 3 metres.
78 LIZ-PBW-2	Fringing reef, between Bird Islet and South Island, Lizard Island, 14 April 1978, P.B. Berents and P.M. Berents, air lifted sediment, 12 metres.	LI-50	Off North Point, Lizard Island, 14 October 1978, J.K. Lowry, mixed algal samples, 3 metres.
78 LIZ-PBW-9	Outer slope, Yonge Reef, 13 April 1978, P.B. Berents, coral rubble, 12 metres.	LI-52	Off North Point, Lizard Island, 14 October 1978, P.C. Terrill, <i>Halimeda</i> , 6 metres.
LI-1	Off Mangrove Beach, Lizard Island, 28 September 1978, J.K. Lowry, mixed algae from bommie, 2 metres.	LI-59	1.6 kilometres SW of Eagle Island, near Lizard Island, 17 October 1978, J.K. Lowry, air lifted sediment from coral fans, rubble and dead coral on reef face and bommies, 4 metres.
LI-2	Watsons Bay, Lizard Island, 29 September 1978, J.K. Lowry and P.C. Terrill, <i>Halophila</i> , <i>Caulerpa</i> , <i>Udotea</i> and drift algae, 7 metres.	LI-61	1.6 kilometres SW of Eagle Island, near Lizard Island, 17 October 1978, J.K. Lowry, sponge sample, with some algae and coral rubble on and below bommies, 4 metres.
LI-11	Reef at western end of Lagoon, Lizard Island, 5 October 1978, J.K. Lowry, C. Short and P.C. Terrill, mixed algal sample, 0-3 metres.	LI-62	1.6 kilometres SW of Eagle Island, near Lizard Island, 17 October 1978, P.C. Terrill, algal sample, predominantly of reds from beneath bommies, with some sponges, 4 metres.
LI-16	Fringing reef, between Bird Islet and South Island, Lizard Island, 7 October 1978, C. Short, filamentous algae, 9 metres.		

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Waisted Blades in Australia?

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ABSTRACT. Waisted tools from two localities in Australia are compared with the better known, flaked waisted blades from New Guinea. In size, shape and type of edge modification, the two Australian samples differ both from each other and from New Guinea specimens. While waisting itself is seen as appearing in Australia through independent invention rather than as a shared concept, other aspects of the technology, which were universal, are seen as preconditions for waisting. These increased the probability of waisting's being invented in the region more than once.

LAMPERT, R.J., 1983. Waisted blades in Australia? Records of the Australian Museum 35(4): 145-151.

The earliest carbon dates of around 40,000 BP from Australia show that the initial human colonization of territories east of the Wallace Line took place in the Late Pleistocene. The sea level was then low enough to join New Guinea, Australia and Tasmania into one land mass, known as Greater Australia, but not low enough to bridge the water barrier separating Greater Australia from the Indonesian islands that form the nearest part of Southeast Asia. Crossing this sea barrier could only have followed the development of suitable watercraft, but other ideas or 'cultural baggage' entering Greater Australia with these early migrants from Southeast Asia cannot easily be recognized.

In addressing this question, Golson (1971) looked for a correspondence in archaeological traits as an indication of the transmission of technological ideas between Southeast Asia and Greater Australia. One trait seen as significant by Golson is the presence of waisting as a hafting aid on certain percussive cutting implements from both sides of the Wallace Line.

'Waisting' is the presence of a pair of opposed flaked notches, one on each long side of an implement. It is a trait most commonly known from New Guinea, where it appears on both edge-ground and flaked tools, known collectively as 'waisted blades'.

At the time of his investigation, Golson was unaware of the presence of waisting on Australian tools and based his comparisons with Southeast Asian tools on New Guinea specimens. However, waisting produced by opposed flaked notches has been recognized on tools from Kangaroo Island, South Australia (Lampert, 1981), and from the Mackay district of Queensland (McCarthy, 1949). In both Australian situations the tools appear as surface finds and are thus almost impossible to date accurately. However, from distributional evidence, the Kangaroo Island tools seem almost certain to be Pleistocene in age (Lampert, 1981).

In view of Golson's argument for waisting as a trait indicating early cultural relationships within New Guinea and beyond, it seems reasonable to examine the proposition that Australian waisted tools are similarly related. Having inspected a sample of 14 waisted tools from Kangaroo Island and more recently a sample of 80 from Mackay, I will compare these with each other and with a group from New Guinea in terms of shape, size and any evidence for function suggested by their working edges.

Characteristics of Tools

New Guinea waisted blades. In the most comprehensive survey of these tools yet carried out, Bulmer (1977) identifies three significant groups. These are: 11 tools from layers dating to around 26,000 BP at the Kosipe open site in the southern highlands; 19 tools from levels dating to a minimum of 12,000 BP at the Yuku site in the highlands; 106 tools from surface sites of unknown age in the Passismanua district of southern New Britain. In comparing these in terms of their shape and size, and type of edge, Bulmer finds some differences between the groups but also a great deal of similarity. Because of their likeness in these same characteristics to unwaisted axe blades, Bulmer argues that both waisted and unwaisted percussive cutting tools belong to the same functional continuum.

Of the three New Guinea groups of waisted blades, I chose those from Kosipe for comparison with the Australian samples, partly because Kosipe tools, being the largest, are the nearest in terms of size to the Australian tools, and partly because the raw metrical data is published (White *et al.*, 1970). All of the flaked waisted tools in the three groups considered by Bulmer have bevelled ends sharpened by either bifacial or unifacial flaking.

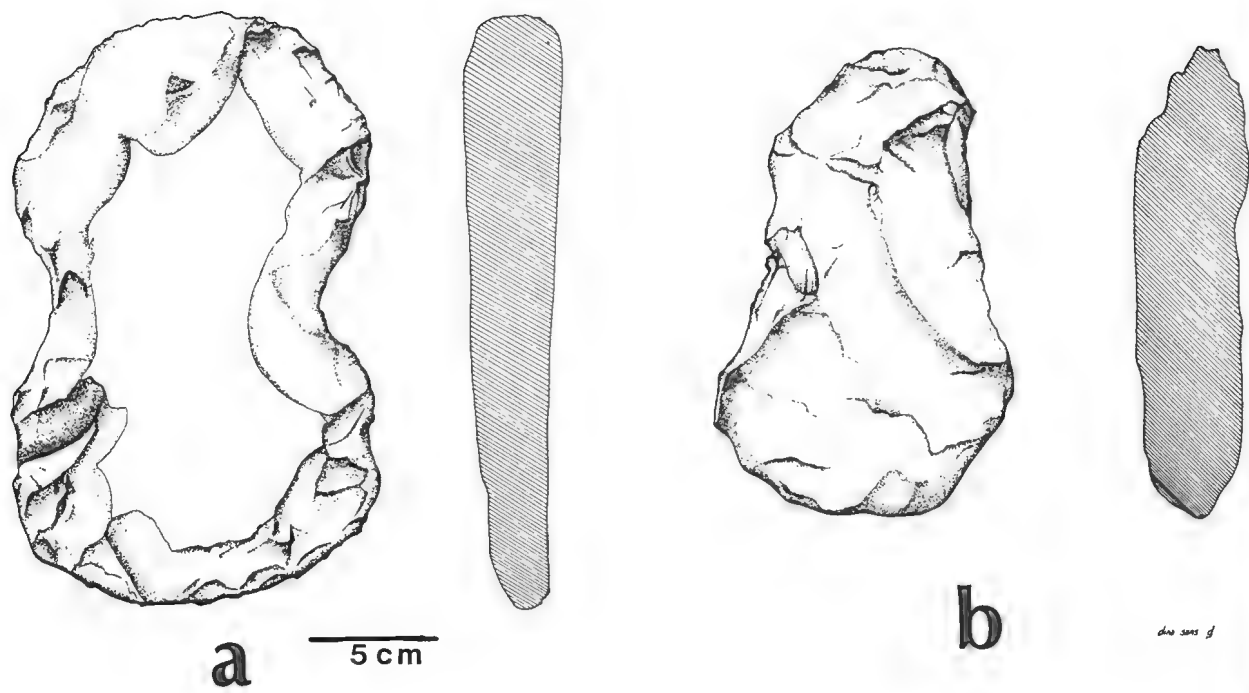


Fig. 1. Mackay waisted tools.

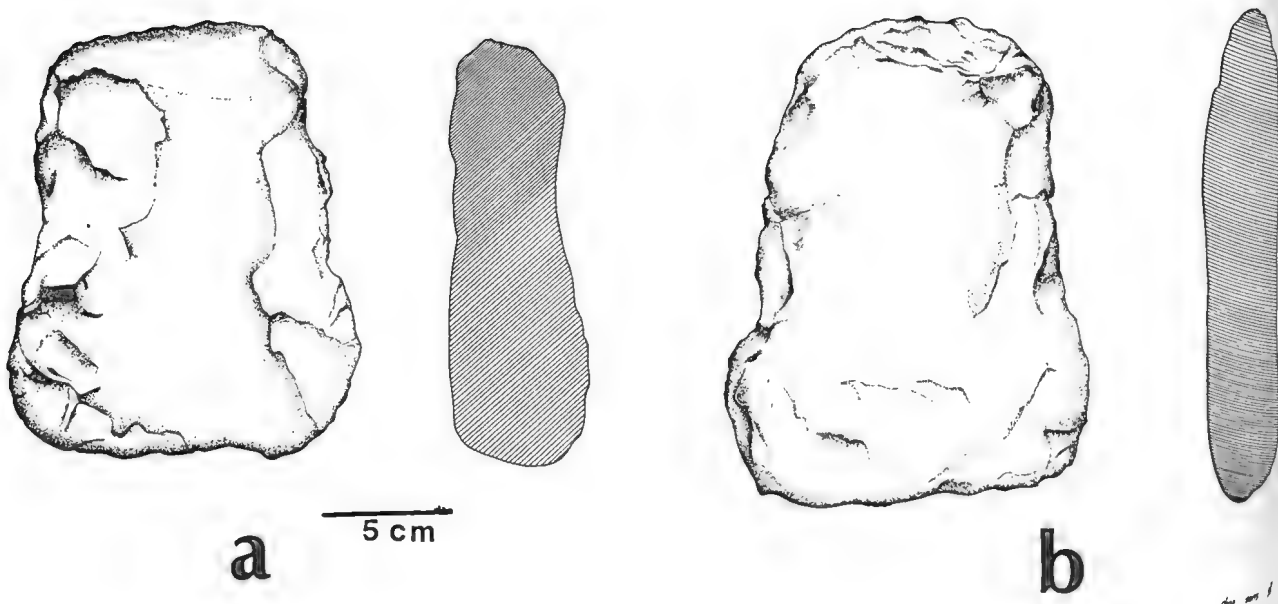


Fig. 2. Mackay waisted tools.

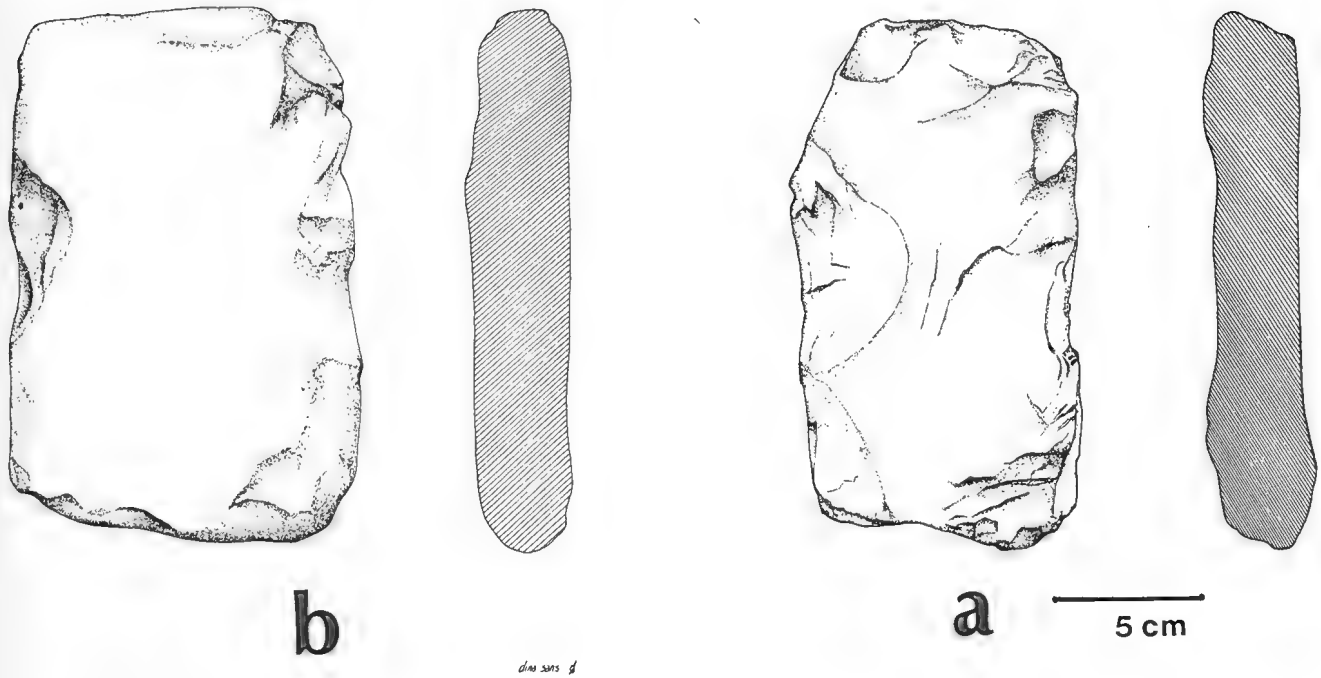


Fig. 3. Mackay waisted tools.

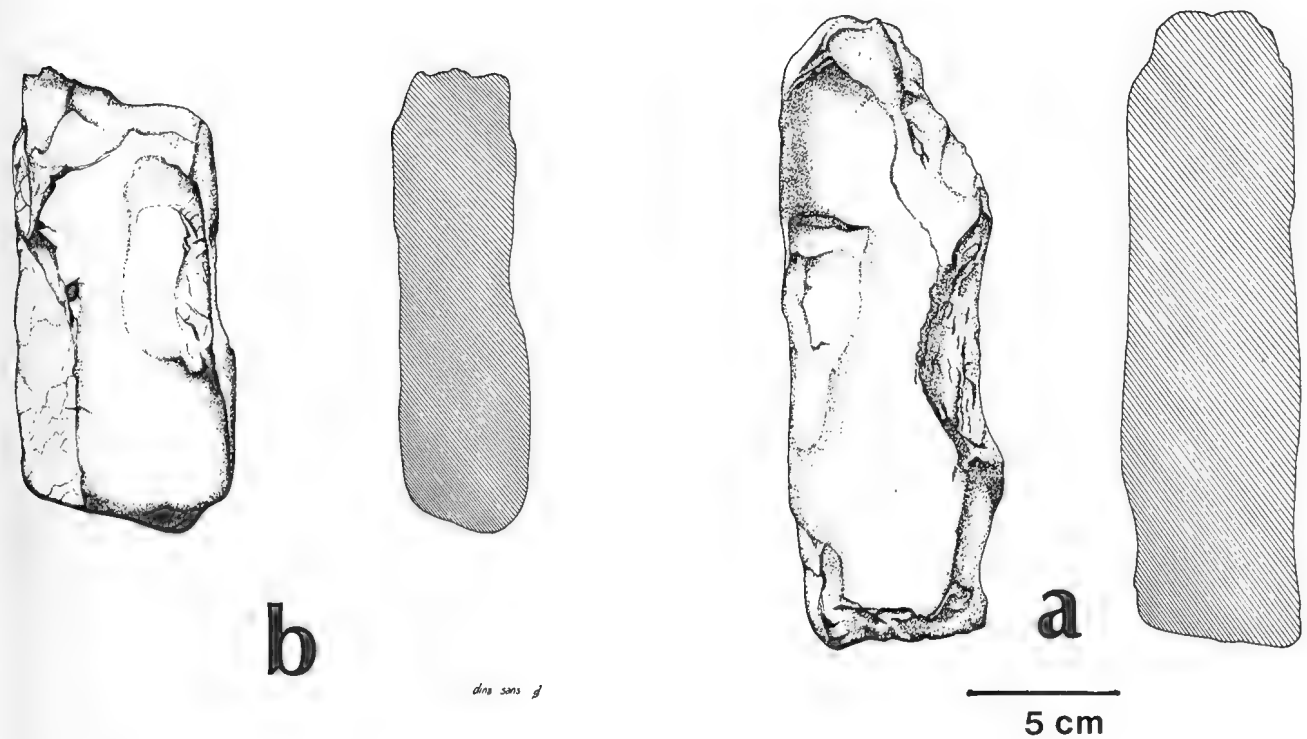
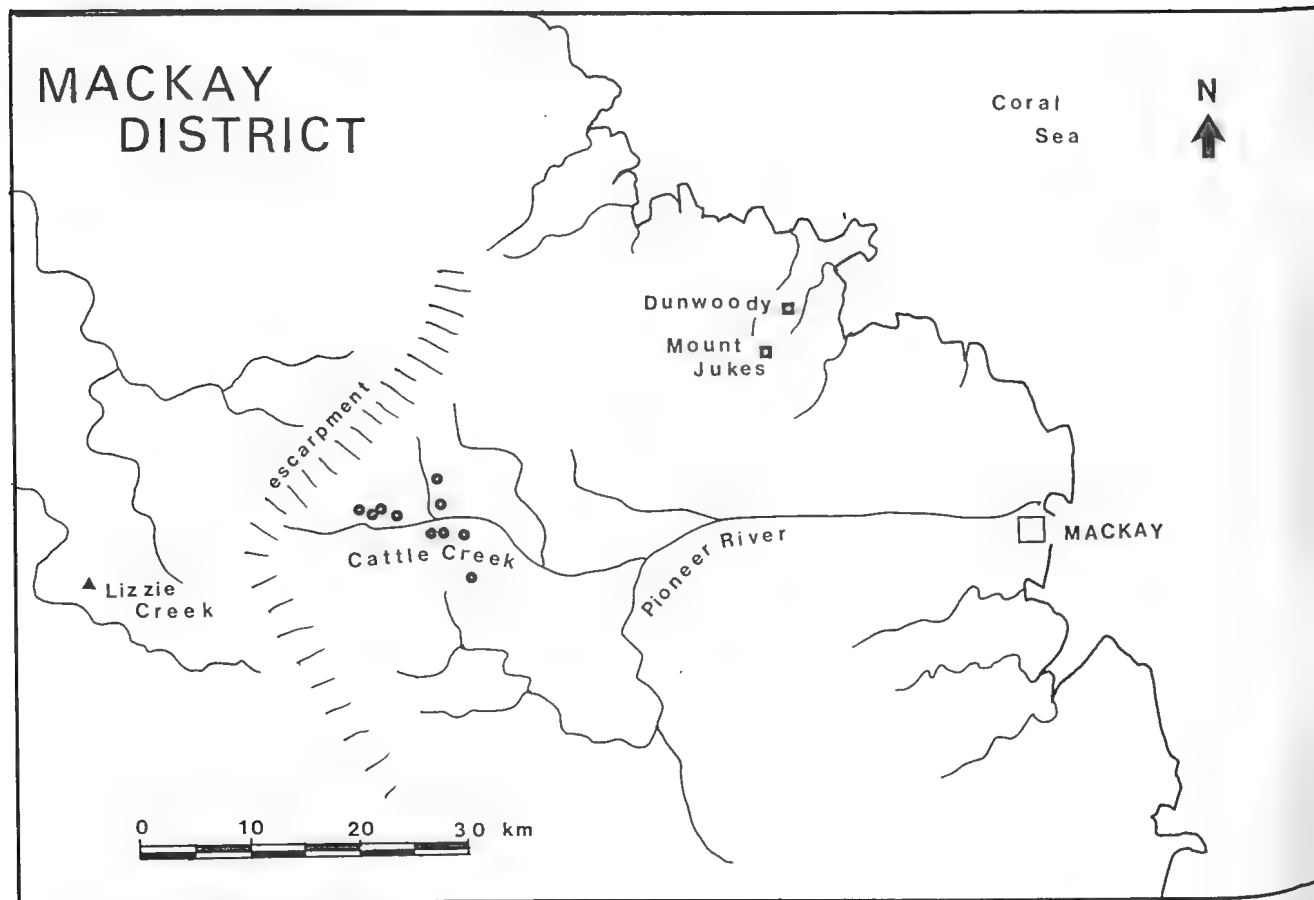


Fig. 4. Mackay waisted tools.



Map 1. Mackay district, Queensland, showing: sites at which waisted tools were found (squares); other sites examined which do not have waisted tools (circles and triangle).

Kangaroo Island. Twenty-four waisted tools have been found on surface sites on Kangaroo Island. Because most were found either near or on Kartan sites, and because they share the same massiveness and are made of the same rock types as Kartan tools, I have suggested (Lampert, 1981) that these waisted tools are part of the Kartan industry and are Pleistocene in age. They show a more varied range of edge modification than do the New Guinea tools, 70% of the functional ends of Kangaroo Island tools being bevelled by flaking, while the remaining 30% are either naturally rounded or squared off along a natural cleavage plane.

Mackay. I visited Mackay in October, 1981, to look more closely at a sample of waisted tools identified initially by McCarthy (1949), my interest being aroused because the few measurements published by McCarthy had suggested that these tools are similar in size and shape to those from Kangaroo Island (Lampert, 1981:191). Because of additional discoveries in recent years, I was able to examine a larger sample than that available to McCarthy. On a total sample of 80 of the Mackay waisted tools, held in two private collections, I recorded the same 10 measurements already taken on the Kosipe and Kangaroo Island specimens (White *et al.*, 1970; Lampert, 1981) and made several observations

that would allow the functional ends of the tools to be described.

I looked also at the distribution of Mackay waisted tools as recorded by their discoverers, finding them to be clustered in quite discrete groups with isolated finds coming to light only rarely. Nearly all were found in the Mount Jukes–Seaforth area 30 km north of Mackay, while only one was located in Cattle Creek Valley, west of Mackay (Map 1). Mr J.H. Williams of Mackay found the Mt. Jukes tools in two major groups: 18 in one paddock on the southern lower slopes and 17 within one acre at Jordans Gap. The largest collection, comprising some 80 tools, was found by E. and N. Dunwoody on their cane farm near Seaforth, some 5 km from Mt. Jukes. All came from a narrow strip of land that is ecotonal between open forest and rain forest, and parallel to a creek about 100 m distant in which permanent water holes persist throughout the dry season. The Dunwoody's say that about half of their collection came from a cultivated area of only 150 × 120 m. I looked carefully over this area and found two small core tools but no other flaked stone. There was, however, naturally occurring stone of the same volcanic type as that of which the tools are made.

An examination of this large sample provides testimony to support McCarthy's view that the artefacts

were hafted by the aid of the two opposed notches, and used as heavy hammers or pounders. The evidence for this function is not only the massiveness of the tools (mean weight: 1.9 kg) but also the shape of their ends and the type of damage these have suffered during use (Figs 1-4). For most tools, blocks of volcanic stone with naturally squared-off ends had been chosen, giving the flat hammer-like striking surface present on 67% of ends. On nearly all of these flat ends, bruising is present around the margins, and flake scars extend away from them to invade the sides of the tool. These modifications must be the result of heavy percussion during use, and are reminiscent of a use wear pattern I have seen on some New Guinea sago pounders, except that gloss is absent. Sharp, bifacially flaked ends, which comprise a further 25% of the sample, could be a more developed form of this same pattern of use wear, the flake scars appearing too irregularly to be a deliberate method of sharpening an edge. Rounded ends, which make up the remaining 8% of the sample, have been formed by numerous small bruises and pits that suggest repeated blows, too light to dislodge flakes visible to the naked eye. Although McCarthy (1949) distinguishes between "hammers" and "blanks" among the Mt. Jukes specimens, I was unable to verify this distinction through my own observations.

In shape, the tools vary from those on which the opposed notches produce the hourglass waisting (e.g. Fig. 1a) typical of Kangaroo Island waisted tools (Lampert, 1981: 192-5); through blocks on which the notches, though still opposed and bifacial, are not deep enough to alter the rectangular outline of the tool (Figs 3a, b); to blocks on which the notches are similarly subdued, but which are elongate and have a squarish lateral cross section (Figs 4a, b).

Exactly what the Mackay tools were used for is currently unknown, but the site locations suggest that people who were based at open forest sites near fresh water used the tools in the exploitation of some product of the rainforest. Using Roth (1904) as his main authority, McCarthy (1949) suggests a number of uses for hammers, including loosening bark from trees, pounding hard nuts, knapping stone and making bark cloth. However, the hafted tools identified by Roth (1904: pls xviii, xix) as being so used show no close relationship to the Mackay waisted tools, particularly in the form of edge damage. I examined these same hammers, collected by Roth, in the Australian Museum (Accession nos E13652 to E13656). All are hafted and made on river pebbles of volcanic stone. The edge damage, which in form is consistent throughout the sample, is a finely pitted flattening at the end of a pebble, like that seen on many unhafted archaeological hammers from sites widespread in Australia (e.g. McCarthy, 1976: 67). Among the Mackay tools, this form of edge damage is most akin to the rounded pitted ends which make up only 8% of the sample. One Roth specimen (E13652) has a single large flake removed, presumably by use, from a face adjoining the working end; whereas multiple flake removal is the most

common type of edge damage on the Mackay tools. I suspect therefore that the Mackay tools, because of this more pronounced form of edge damage, served for much heavier work than that described by Roth. Nor are the edges of the Mackay tools like those of the bevelled pounder, used possibly for the preparation of fern root as a food in south-eastern Queensland (Kamminga, 1981; Gillieson and Hall, 1982), which again were used for much lighter pounding than were the Mackay tools. A closer identification of function might emerge from further studies, both of the ethnographic evidence for rainforest economies and of the rainforest environment itself, and through experiments designed to replicate the type of edge damage.

Statistical Analysis

The relationships between the groups of waisted tools from Australia and New Guinea were investigated through manipulating the data already described.

Multivariate analyses and significance tests indicate no significant differences between two separate col-

Table 1. Mean (\bar{x}) and standard deviation (s) scores for groups of waisted tools.

N	18	60	14	11
Length ₁ :				
\bar{x}	184.4	186.4	206.2	126.8
s	20.5	24.8	28.7	34.4
Length ₂ :				
\bar{x}	86.7	91.9	100.2	41.5
s	13.6	16.4	17.2	21.1
Length ₃ :				
\bar{x}	43.1	41.5	41.2	13.0
s	11.4	10.7	6.9	4.7
Length ₄ :				
\bar{x}	47.1	46.3	51.0	48.1
s	17.6	11.6	9.3	32.9
Breadth ₁ :				
\bar{x}	108.6	107.0	120.1	60.8
s	19.1	14.4	19.0	24.0
Breadth ₂ :				
\bar{x}	118.4	119.5	141.9	64.9
s	25.1	17.2	24.4	24.8
Breadth ₃ :				
\bar{x}	133.4	130.7	155.5	97.1
s	18.5	16.1	17.4	31.9
Height ₁ :				
\bar{x}	45.6	43.5	42.1	23.5
s	14.9	9.2	7.6	9.2
Height ₂ :				
\bar{x}	42.2	42.8	40.6	21.0
s	11.4	9.1	7.4	7.1
Height ₃ :				
\bar{x}	40.3	42.8	40.6	21.4
s	14.3	10.6	9.1	7.9

Table 2a. Matrix of pairwise F ratios (Mahalanobis distances).

	Mt. Jukes	Kangaroo Island	Dunwoody
Kangaroo I.	2.62		
Dunwoody	1.00	2.66	
Kosipe	11.00	11.31	13.86

Table 2b. Matrix of differences significant (S) at the .001 level.

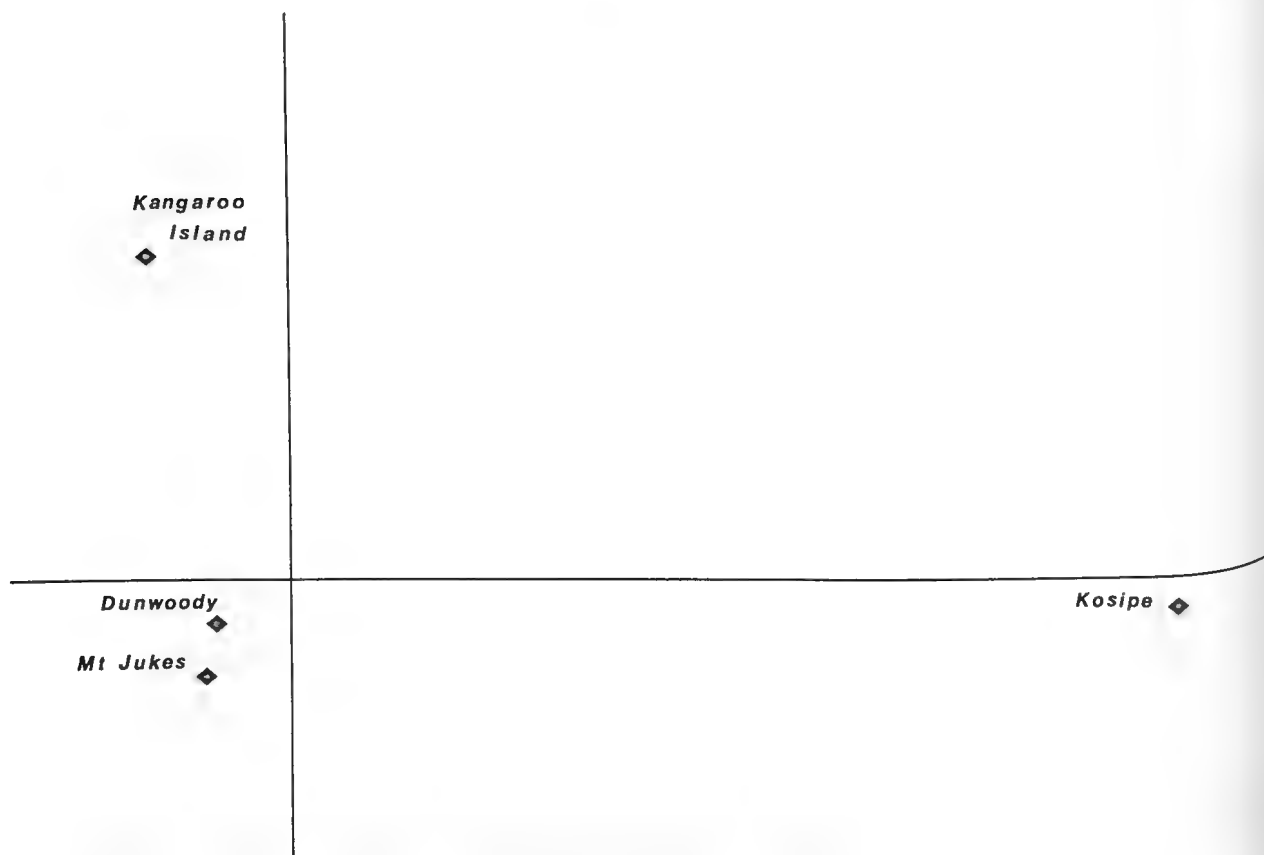
	Mt. Jukes	Kangaroo Island	Dunwoody
Kangaroo I.	S		
Dunwoody	—	S	
Kosipe	S	S	S

lections of Mackay waisted tools found only a few kilometres apart at Mt. Jukes and Dunwoody. However, the Mackay, Kangaroo Island and Kosipe tools all differ significantly from one another (Tables 2a, b). These localities are separated geographically by long distances that must have crossed the territories of numerous groups of people, and in the intervening areas waisted tools are extremely rare. Even if the tools from

the three isolated localities were contemporary, which is a doubtful proposition, it is hardly likely under such circumstances that the tools, though related, would be closely like each other. Therefore, I find the difference revealed by significance tests to be unremarkable, as Wright (1974) notes for other tools from widely spaced Australian sites.

More appropriate here are statistics that judge the amount of variation (Wright, 1974: 171), or compare archaeological distances, such as techniques that attempt to cluster sites and portray the results graphically for visual evaluation. Discriminant analysis of the waisted tools shows Kangaroo Island fairly close to the two Mackay sites and Kosipe at a considerably greater distance from either (Fig. 5). This grouping is suggested also by examining the functionally sensitive ends of the tools. Those from Mackay have a high percentage of flat ends, those from Kangaroo Island very few, and those from Kosipe none.

Looking a little more closely at the discriminant analysis plot (Fig. 5), the Mackay sites and Kangaroo Island are separated from Kosipe along the horizontal axis (Function 1), whereas along the vertical axis (Function 2) Kangaroo Island is the outlier. An inspection of the raw output tables shows that size, particularly length, is the main component of the first discriminant function, while the second is possibly a reflection of shape. Kosipe waisted tools are significantly smaller than those from the Australian sites. The uniqueness of Kangaroo Island tools is

**Fig. 5.** Comparison of waisted tool groups through discriminant analysis.

possibly due to shape, though this is not readily apparent from an inspection of other data (e.g. Table 1).

Also relevant here is another group of New Guinea waisted tools found recently on raised coral terraces in the Huon District (Groube, pers. comm.). These too have sharp rather than flat ends, but in main dimensions appear to resemble more closely the Australian tools than they do those from Kosipe.

Discussion

Different in size, shape and probably function, these isolated groups of tools have only waisting as a common trait. Does the presence of waisting unite them culturally at a broader level of comparison, as Golson (1971) argues for waisted tools in New Guinea and Southeast Asia? In New Guinea, at least, waisting is fairly widespread, with localities of occurrence separated by areas which are not well known archaeologically. In Australia, however, definite suites of waisted tools have been found at only two localities some 2000 km apart, and the intervening areas are better known archaeologically. Therefore, while the New Guinea sites are possibly linked by a shared concept this could not reasonably be argued for Australia. It would mean accepting the view that, because of common origins, some cultural traits had spread over a vast area and then lain dormant, perhaps for several thousands of years. Later, these traits had emerged in widely separated localities. This proposition I find completely implausible.

An alternative hypothesis that seems more attractive is the independent invention of waisting as a hafting device to meet specific needs both on Kangaroo Island and in the Mackay district, these two groups of tools not being directly related either to each other or to New Guinea waisted blades. As an even more acceptable alternative, I propose a modified version of this hypothesis. Could it be that a broadly similar level of stone technology, which has been demonstrated for the Southeast Asian-Greater Australian region (Hayden, 1977), allows a high probability for the independent invention of fairly simple ideas like waisting as a hafting aid? While the idea of waisting itself might not be transmitted directly between isolated groups of people, the preconditions for waisting might be spread widely in the region. Indeed, for waisting there are preconditions more specific than the broadly similar level of stone technology mentioned above. The concept of attaching a heavy blade, used for hammering or cutting, transversely to a wooden handle is widespread. Of greater importance perhaps is the type of handle used in the region and the manner in which it is attached to the stone head. Throughout Aboriginal Australia in recent times, axes were hafted by "bending a strip of split vine or cane, bark or wood cut from a sapling or branch, round the axe head, and sealing the joint with gum cement . . ." The handle is bound with twine at several points . . ." (McCarthy, 1976:47). A flexible handle of this kind wrapped around the reduced waist of a tool

would produce a secure grip, as Bulmer (1977) has argued for the hafting of New Guinea waisted blades.

In conclusion, I do not see the Australian waisted tools and those from New Guinea as evidence for these areas' sharing a common idea of waisting. Rather, it is a universal method of hafting, using a flexible vine or split sapling wrapped transversely around a tool, that has increased the probability of waisting's being invented independently more than once.

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First Record of *Amphidromus* from Australia, with Anatomical Notes on Several Species (Mollusca:Pulmonata:Camaenidae)

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ABSTRACT. *Amphidromus cognatus* Fulton, 1907, described from a single specimen without locality data, is here recorded from several places north of Darwin in the Northern Territory. This is the first record from Australia of this South-east Asian to Timor genus of arboreal snails. Dissections of the genotype, *Amphidromus perversus* (Linné, 1758) from Bali and *A. poecilochrous jaeckeli* Laidlaw, 1954, from Flores, Indonesia, provide comparative data on genital and radular structures of *A. cognatus*. There are easily observable species differences in the terminal genitalia, although shell variation is great and confusing.

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Amphidromus Albers, 1850, is a genus of colourful tree-dwelling land snails that has long been popular with shell collectors. Species now referred to this genus are known in the region from the Garo and Khasi Hills of Assam throughout South-east Asia and Indonesia as far as the Celebes, Banda Islands, Timor, and Tanimber Islands. The northern limits seem to be the Southern Philippines (Mindanao and the Balabac-Palawan chain), Vietnam, Thailand, Burma and Assam. *Amphidromus* is replaced in New Guinea and parts of Wallacea by the papuinid complex of genera (Solem, 1959: 274, fig. 21). The occurrence of *Amphidromus* on Melville and Bathurst Islands and the Cobourg Peninsula, Northern Territory, Australia is thus a significant range extension.

Early well-illustrated studies by Fulton (1896) and Pilsbry (1900) are still the standard references for identification of *Amphidromus* species and colour forms from shell features. The synoptic catalogue of Laidlaw and Solem (1961) incorporates post-1900 literature and summarizes current knowledge. Description of two colour varieties from Komodo Islands, Indonesia (Djajasasmita, 1963); a review of variation in Thailand taxa (Solem, 1965); brief anatomical notes on *A. palaceus* (Mousson, 1848), *A. javanicus* (Sowerby, 1841), *A. heerianus* (Pfeiffer, 1871), and *A. porcellanus* (Mousson, 1848) by Bishop (1977), and on the terminal genitalia of *A. poecilochrous jaeckeli* Laidlaw, 1954 by Minato (1979), are the only subsequent papers other than catalogue listings in faunal checklists. The most significant contribution to knowledge of *Amphidromus* remains the masterly account of variation in East Timor species by Haniel (1921). Subsequent commentaries by Rensch (1931,

1935) on the systematics of the Timor populations only emphasize the complex nature of local variation and the inadequacies of using shell morphology alone to determine species limits.

The data on anatomical variation presented below, when interpreted with the aid of concepts on species recognition structures developed in studies of Australian camaenids (Solem, 1979, 1981a,b), confirm that variations in the terminal genital structures are most useful in recognizing species limits. Radular teeth of *Amphidromus* show several unique features that depart significantly from the normal pattern found in the family Camaenidae.

ABBREVIATIONS

AM:	Australian Museum, Sydney.
BM(NH):	British Museum (Natural History), London.
FMNH:	Field Museum of Natural History, Chicago.

Family CAMAENIDAE Pilsbry, 1893

Genus *Amphidromus* Albers, 1850

Amphidromus cognatus Fulton, 1907

Figs 1-7, 14, 23, 24

Amphidromus cognatus Fulton, 1907: 151, pl. IX, fig. 7.—
Laidlaw and Solem, 1961: 592, 610.

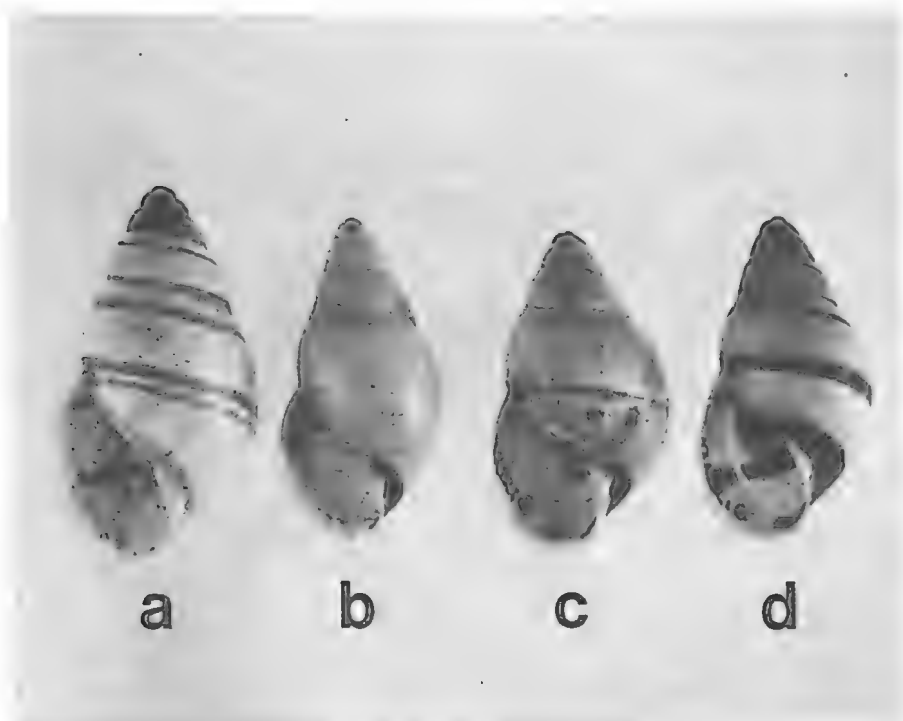


Fig. 1. Shells of *Amphidromus cognatus* Fulton. a, trees near beach, Bathurst I., near Darwin, Northern Territory, Australia, AM C.122528; b-d, on trees, Milikapiti Bay, Melville I., Northern Territory, Australia, AM C.121216. Height of largest shell is 29.7 mm.

Holotype. BM(NH) 1907.5.3.122.

Type locality. Port Essington, Cobourg Peninsula, Northern Territory, Australia (here restricted).

Records. Port Essington, Cobourg Peninsula (2 adults: BM [NH] 51.11.15.37, AM C.122527); alive on trees near beach, Bathurst I., near Darwin (1 adult, AM C.122528, collected by P. Carrol in 1976-1977); Milikapiti Bay, rain forest pocket between waterpumps, c. 500 m from beach, Melville I., near Darwin (22 adults, 20 juveniles, AM C.121216, collected by V. Kessner, 5 April 1980); Milikapiti Bay, rain forest behind pumps, Melville I. (15 live adults, 6 live juveniles, AM C.126706, FMNH 198760, collected by V. Kessner, 11 November 1980); 10 km from Milikapiti Bay on way to Kerslake, Melville I. (3 dead adults, AM C.126705, collected by Vince Kessner, 10 December 1980); along creek at bridge 3-4 km from Paru, Melville I., near Darwin (2 adults, 4 juveniles, AM C.121192, collected by P.H. Colman and V. Kessner, 21 March 1980).

Description of shell. Relatively small, sinistral, height 20.9-32.7 mm (mean 25.91 mm), diameter 12.15-17 mm (mean 14.35 mm). H/D ratio 1.56-2.12 (mean 1.80). Whorl count $4\frac{7}{8}$ to 6 (mean $5\frac{3}{8}$), sutures shallow, whorl contour rather flat. Lip very weakly to moderately expanded, sharply reflected, a very narrow umbilical chink remaining. Shell surface with only occasional weak radial growth lines. Colour pattern variable.

All specimens have the umbilical chink interior showing only the ground colour. A prominent spiral band of chocolate brown (except in the single Bathurst Island specimen, Fig. 1a) lies on the columella around the umbilicus. Additive colour elements present on some

to most specimens may include a peripheral spiral chocolate brown colour band (Fig. 1a; d), a distinctly subsutural chocolate brown colour band (Fig. 1a, d), and a purplish brown apical suffusion (Fig. 1a, c, d). The width of the upper spiral bands and columellar colour band vary (Fig. 1). The additive elements do not appear completely linked. While no specimen with a prominent spire suffusion lacks the peripheral colour band, the subsutural band may or may not be present with spire suffusion. No specimens have any of the spirals broken up into flammulations. Lip white or with a faint yellowish cast. Ground colour medium yellow in fresh examples, on body whorl occasionally showing tonal irregularities along growth lines, fading on spire and in worn examples.

Distribution and habitat. Modern records from Bathurst and Melville Islands near Darwin, Northern Territory, are in addition to the pre-1850 record from Port Essington, Cobourg Peninsula. Some of the specimens collected alive on Melville Island have been taken from the plant *Opilia amentacea* Roxburgh.

Remarks. The unlocalized holotype and two specimens of *Amphidromus cognatus* from Port Essington all have the complete suite of colour features, are three of the four specimens over 30 mm in shell height, and have the shell lip more strongly reflected and more broadly expanded. The restriction of the type locality to Port Essington is based on this identity of material. It is quite probable that all three were collected at the same time, but that the holotype subsequently became separated from its locality data and thus was

described as "locality unknown". Specimens with full colour elements from Melville Island differ from the Port Essington specimen only in their noticeably smaller size (Fig. 1b-d), thinner shell, and much less broadly reflected and expanded shell lip.

The Bathurst Island example (Fig. 1a) also has a full colour complement on the spire, except that the peripheral colour band is split into a wider upper and narrower lower portion. The columellar colour band is absent. Its lip is strongly expanded, and it is 29.7 mm high, with $5\frac{1}{2} +$ whorls, thus almost equalling the size of the types.

Of the dead Melville Island examples taken in April, 1980, 18 adults and 13 juveniles could be scored as to colour pattern. Four adults and eight juveniles were so worn that either no colour pattern was left, or only partial traces existed. Of the juveniles, 5 have a weak subsutural and umbilical patch; 4 have apical colour suffusion, a strong peripheral, and an enlarged to double width umbilical colour band; and 4 have a heavy spire suffusion, heavy subsutural, heavy peripheral, and prominent umbilical colour band. Of the adults, 5 have a heavy spire suffusion, medium to strong peripheral, weak to strong subsutural, and prominent umbilical colour band (Fig. 1d); 1 has a weak peripheral colour band that fades out before the lip edge (Fig. 1c), and a prominent umbilical colour band; and 14 have only the umbilical colour band (Fig. 1b). Size variation in the 22 dead adults collected 5 April 1980 (AM C.121216) is:

	Mean	S.E.M.	Range
Shell height	25.90 mm	0.428	21.55–29.35 mm
Shell diameter	14.42 mm	0.206	12.3–16.75 mm
H/D ratio	1.80	0.013	1.68–1.90
Whorls	$5\frac{1}{2}$	—	5 to $5\frac{1}{2}$
Aperture length	13.33 mm	0.200	11.6–15.0 mm

The two live adults (AM C.121192) collected 21 March 1980 are slightly smaller than average, but typical.

The live material from Milikapiti Bay taken 11 November 1980 included 15 live adults, several of which had only very thinly expanded lips. Loose eggs in the preservative indicated that at least one animal was in the process of egg laying. Dissection of four adults failed to discover any eggs in the female tract. Colour variation in the adult shells was quite similar to that in the dead April collections. Of the 15 adult specimens, 4 had only the umbilical patch and in one of these it was very weak; 4 had a weak spire suffusion and prominent umbilical patch; 1 had a weak spire suffusion, weak subsutural band, and prominent umbilical patch, 1 had a heavy spire suffusion, prominent peripheral band, and prominent umbilical patch; 3 had all colour components; and 1 had all colour components with the bands widened.

Size variation in the live collected adults was extensive:

	Mean	S.E.M.	Range
Shell height	25.17 mm	0.756	20.9–32.7 mm
Shell diameter	13.69 mm	0.260	12.15–15.7 mm
H/D ratio	1.83	0.036	1.56–2.12
Whorls	$5\frac{1}{4} +$	—	$4\frac{1}{2}$ to 6
Aperture length	13.07 mm	0.322	10.9–15.5 mm

The total size range is clearly extended, but the mean differences are not significant. The three dead adults from on the way to Kerslake had all colour components and were within the range of variation for shell measurements.

Determining the nearest relatives of *Amphidromus cognatus* must await anatomical studies of Timor to Celebes species. Although Haniel (1921) provided much data on external aspects of the terminal genitalia, and illustrated variation ranges for several species, he did not discuss or illustrate the interior surfaces of the terminal genitalia, which is where the species recognition structures are located in the Camaenidae.

On conchological grounds, the most conspicuous species differences lie in the nature of the colour pattern. *Amphidromus cognatus* has the umbilical chink showing shell ground colour only and the umbilical band is sharply defined. All of the colour bands are chocolate brown, when present. Taxa such as *A. laevis* (Müller, 1774), *A. inconstans* Fulton, 1898, *A. contrarius* (Müller, 1774), and *A. columellaris* Möllendorff, 1892, have the colour extending into the umbilical chink (*A. columellaris*), bands of different colours on the shell (*A. laevis*), or strikingly flammulated colour patterns (*A. columellaris*, *A. inconstans*, *A. contrarius*). There are also clear differences in the way that the lip is expanded, in how the umbilical reflection terminates and in whorl contours. Unfortunately, these are difficult to communicate verbally, and would require extensive illustrations to document. Fortunately, the colour differences are adequate for identification.

Amphidromus perversus (Linné, 1758)

var. *interruptus* (Müller, 1774)

Figs 8–9, 20–21

Helix perversa Linné, 1758: 772.—locality unknown.

Amphidromus perversus.—Laidlaw and Solem, 1961:533–534.

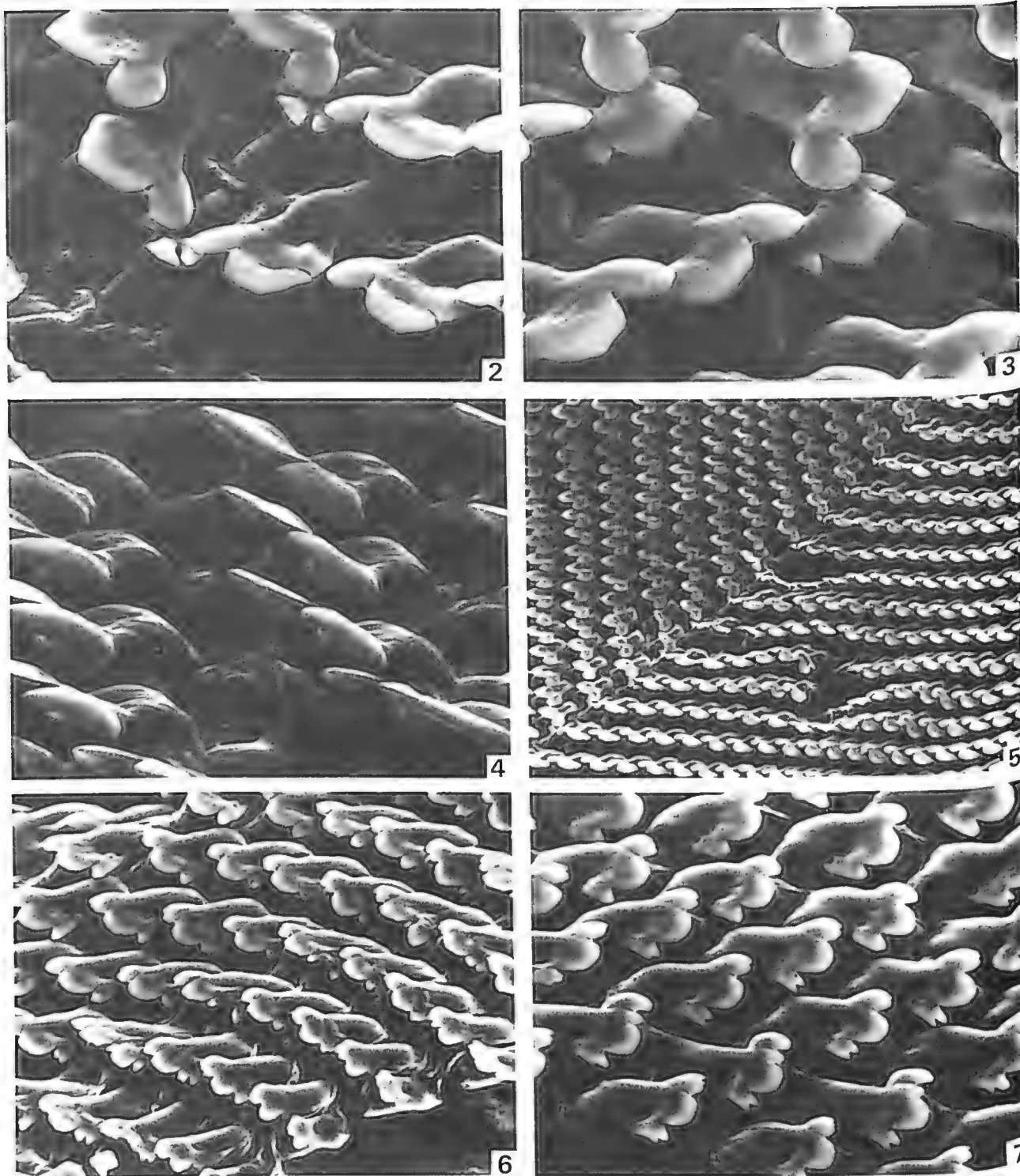
Material. Sanur, 50–200 metres from beach, Bali, Indonesia (8 adults, 3 juveniles, FMNH 198757, collected by Renate Wittig Skinner 5–17 May 1977).

Remarks: Both sinistral and dextral individuals, all referable to the colour form *interruptus* (Müller, 1774), were available.

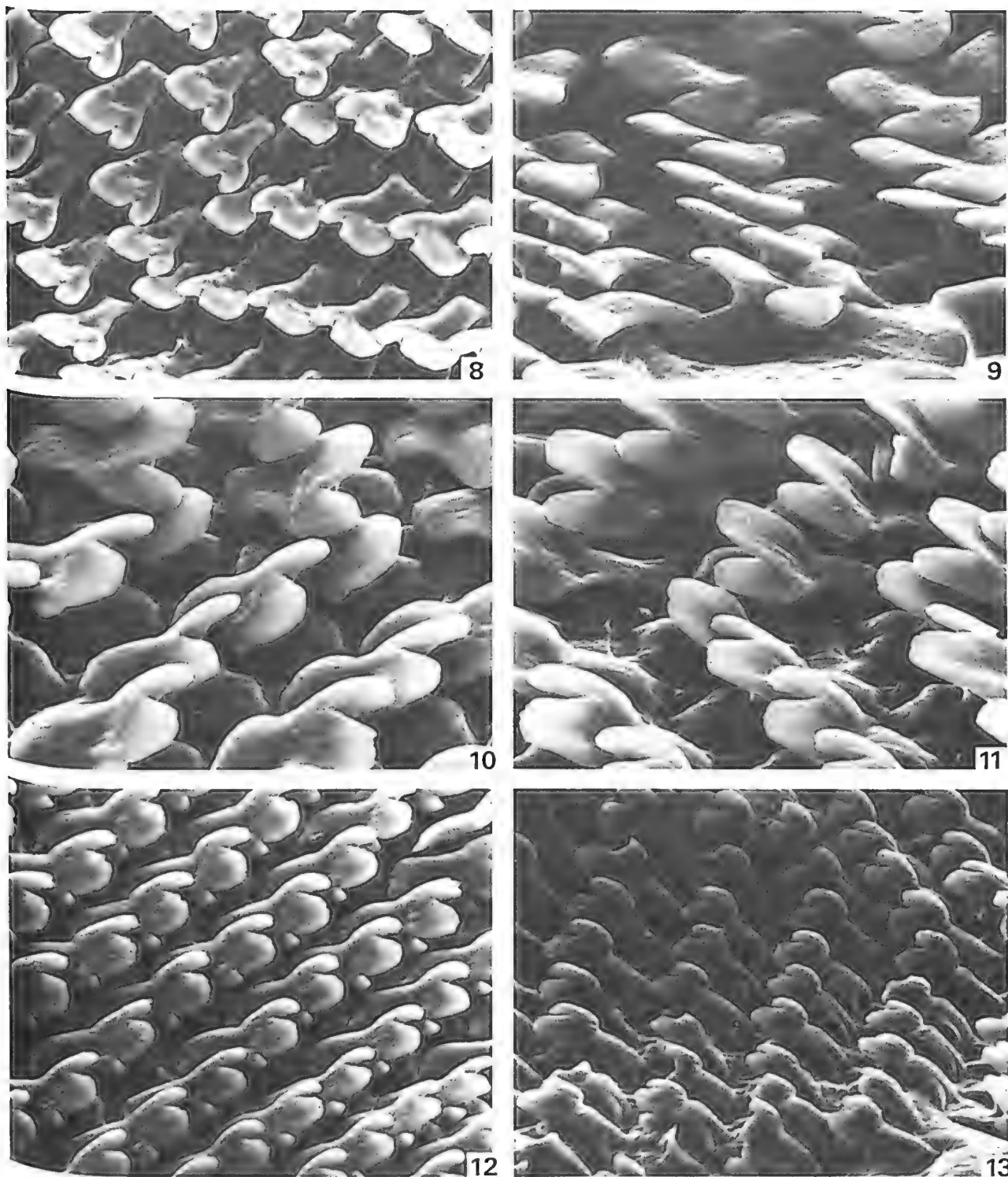
Amphidromus poecilochrous jaeckeli Laidlaw, 1954

Figs 10–13, 15, 22

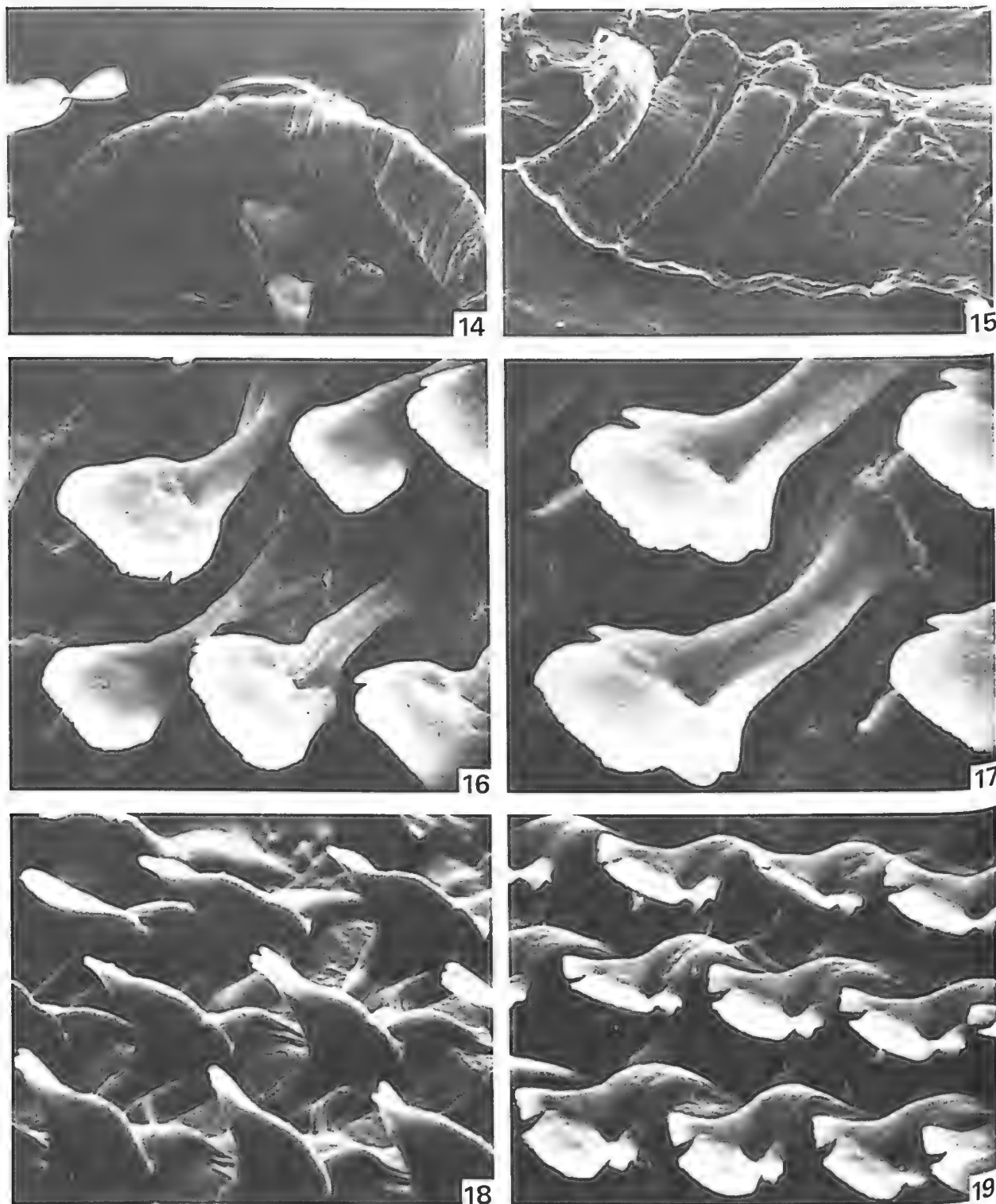
Amphidromus contrarius floresii.—Haltcnorth and Jaeckel, 1940: 174–175, figs 3, 4—Kampung Mosena, West Flores, Indonesia (not Bartsch, 1917).



Figs 2-7. Radular teeth of *Amphidromus cognatus* Fulton. Melville I., Northern Territory, Australia. AM C.121192. 2, 4, 5, 6, are Dissection A. 3, 7, are Dissection B. 2, Rachidian and early laterals, 810 X. 3, Rachidian and early laterals, 907 X. 4, Low angle view of rachidian and early laterals, 1,150 X. 5, Part row view from high posterior angle, 160 X. 6, Outer marginal teeth, 405 X. 7, Mid-marginal teeth, 480 X.



Figs 8-13. Radular teeth of *Amphidromus perversus* (Linné), and *A. poecilochrous jaeckeli* Laidlaw. 8-9, *A. perversus* (Linné). Sanur, Bali, Indonesia, FMNH 198757. 8, Rachidian and several laterals showing variation in shape of anterior basal plate, 410 X. 9, Laterals from left side of radula showing deflection of anterior basal plate margin, 800 X. 10-13, *A. p. jaeckeli* Laidlaw. Konga, Flores, Indonesia, FMNH 198758. 10 and 12 from Dissection A, 11 and 13 from Dissection B. 10, Rachidian and early laterals showing presence of ectocone and anterior basal plate margin deflection, 860 X. 11, Rachidian and early laterals showing absence of ectocones on these early laterals, 780 X. 12, Lateromarginal transition area showing change in basal plate length, 465 X. 13, Outermost marginals from right side of radula, 415 X.



Figs 14-19. Jaws of *Amphidromus* and radula of *Papuina phaeostoma medinensis* Rensch. 14, Jaw of *Amphidromus cognatus* Fulton, 50 X. 15, Detail of jaw of *A. p. jaeckeli* Laidlaw. Note worn tips on upper margin. 152 X. 16-19, *Papuina phaeostoma medinensis* Rensch. 80 miles southeast of Kavieng Village, New Ireland, Bismarck Archipelago (3°02' 30"S, 151° 40'E), FMNH 168394. 16, Rachidian and first laterals in near-vertical view showing anterior basal plate margins, 930 X. 17, Mid-lateral teeth showing serrated mesocone margin and enlargement of endocone (lower) and ectocone (upper), 1,075 X. 18, Lateral teeth viewed from a posterior about 45° angle showing deflection of anterior basal plate, 850 X. 19, High angle view of mid-lateral teeth showing basal plate anterior deflection, 660 X.

Amphidromus contrarius jaeckeli Laidlaw, in Butot, 1954: 106–107, figs 2, 3—Komodo Island, Indonesia.
Amphidromus poecilochrous jaeckeli.—Laidlaw and Solem, 1961: 569–570, 631, fig. 16A; Minato, 1979: 15–17.

Material. Hill near Konga, Flores, Indonesia (3 live adults, FMNH 198758, collected by Renate Wittig Skinner June 1975).

Remarks. The three specimens available, except for having the ground colour extend partly onto the reflected lip, agree with the type illustrations and are thus referred to this subspecies.

Radular Structure

Previous observations on the radula of *Amphidromus* have focused on the angled nature of the rows, and the pattern of cusp shape. Haniel (1921: 49–57, figs 14–21) indicated that there was considerable minor variation in the cusping of the rachidian tooth, but seriously misinterpreted the anterior basal plate margin because of the tooth row overlap inherent in vertical viewing with optical equipment. Bishop (1977: fig. 2) showed only outlines of anterior cusp margins.

Within the context of the Camaenidae, the radula of *Amphidromus* is highly modified, correlating with the arboreal habitat and microfloral food. The only clear indication that this tooth form is derived from the basic camaenid pattern can be seen in teeth approximately midway on the radula between the rachidian and outermost marginals. In *A. p. jaeckeli* (Fig. 12), the persistence of a simple inter-row basal support mechanism at the point of lateral marginal transition can be seen. At the upper right of this illustration, one tooth is angled, showing the altered anterior margin of the tooth, while the next tooth in the same row has the same margin resting on the posterior basal plate of the next tooth in line. In the lower left of this illustration, the basal plates have become noticeably shortened, the posterior basal margin is receding, and the pattern evident in outer marginals of a bifurcated, non-interacting anterior margin (Fig. 13) is set.

Basic row shape in all three species examined agrees with that of *A. cognatus* (Fig. 5)—V-shaped, with the arms of the V directed anteriorly. The rachidian tooth is greatly reduced in size and highly variable in cusp shape (Figs 2, 3, 8, 10, 11). Such variation in cusping on teeth of reduced size, and hence probably reduced function, is well-documented in other land snail taxa, for example, in the athoracophorid slug, *Aneitea* (Solem, 1959: 47). In *A. perversus* (Fig. 8), the rachidian is broadly monocuspid and less reduced in size than in the specimens of *A. p. jaeckeli* (Figs 10, 11). One of these has larger ectocones than the other, and I presume that examination of additional material would increase the range of variation. A much greater contrast was observed in the two specimens of *A. cognatus* (Figs 2, 3). In one specimen (Fig. 3) the mesocone is broad and with truncated posterior cusp margin; in the other (Fig. 2) the mesocone is greatly reduced in size to a Y-shaped nubbin. Both examples have relatively prominent ectocones on the rachidian. When observed from a

lower viewing angle, the cusps are seen to be elevated at almost a 90° angle, but their tips lie distinctly below the plane of the surrounding laterals and thus probably do not function in feeding.

Structure of the lateral teeth is consistent in all three species. Two cusps, a mesocone and an endocone, with the latter distinctly narrower, are elevated in the same cutting plane (Figs 4, 5, 8, 9, 10). This contrasts greatly with the pattern observed in arboreal enids (Solem, 1973: figs 9, 11, 12) and partulids (*ibid.*, figs 13–16, 18, 20) where the two-cusp pattern involves striking differences in both the plane of highest elevation for each cusp and the identity of the second cusp. In these taxa, the mesocone makes initial contact with the food surface followed a microsecond later by an equally elevated ectocone, giving two scrapes from the same tooth. In both of these families there is great overlap between basal plates (*ibid.*, figs 7, 12, 13, 15, 16, 18, 20, 21). In the Partulidae, the inter-row support involves sliding along a significant surface length, while in the Enidae (*ibid.*, fig. 7) there is a more traditional raised point of interlock. *Amphidromus* shows a gross difference (Figs 2, 4, 6, 8, 9, 11). There is, for the lateral teeth, no inter-row support system. Instead, the anterior margin of each lateral tooth is sharply deflected downward (Fig. 4) with its anterior tip lying between the posterior margins of two teeth in the next row. Presumably this curved anterior margin is correlated with surface curvature on the underlying support cartilage during functional rotation of the radular ribbon into the mouth during a feeding stroke. This support system and the elaboration of an endocone into a *simultaneous* cutting edge are two features that I am not aware of being present in any other family of arboreal land snails. Previous illustrations have shown the posterior basal plate margin as abruptly truncated in *Amphidromus*, as the sharply narrowed anterior deflection would be hidden in vertical view by the cusps of the next anterior row.

A modification of this pattern is seen in *Papuina phaeostoma medinensis* from Kavieng, New Ireland, Bismarck Archipelago (Figs 16–19). The central and early laterals are almost monocuspid (Fig. 16), with only a slight endocone trace. After the first few laterals, there is significant ectoconal enlargement and endoconal development (Fig. 17). Most of the functioning laterals (Fig. 18) show the same anterior margin deflection reported above for *Amphidromus*, although the earliest laterals (Solem, 1974: 136) have a simpler structure (Fig. 16). Early marginals (Fig. 19) show enlargement of the side cusps and accentuation of the anterior deflection. This suggests, as has been hypothesized previously on other grounds, that *Amphidromus* and the papuinid complex of genera are parallel experiments in arboreal living, but probably are not monophyletic.

The process of transition to marginal teeth in *Amphidromus* (Fig. 12) can be pin-pointed to a small region of basal plate shortening. In all three species, gradual development of an ectocone has been proceeding for a number of teeth, accompanied by size

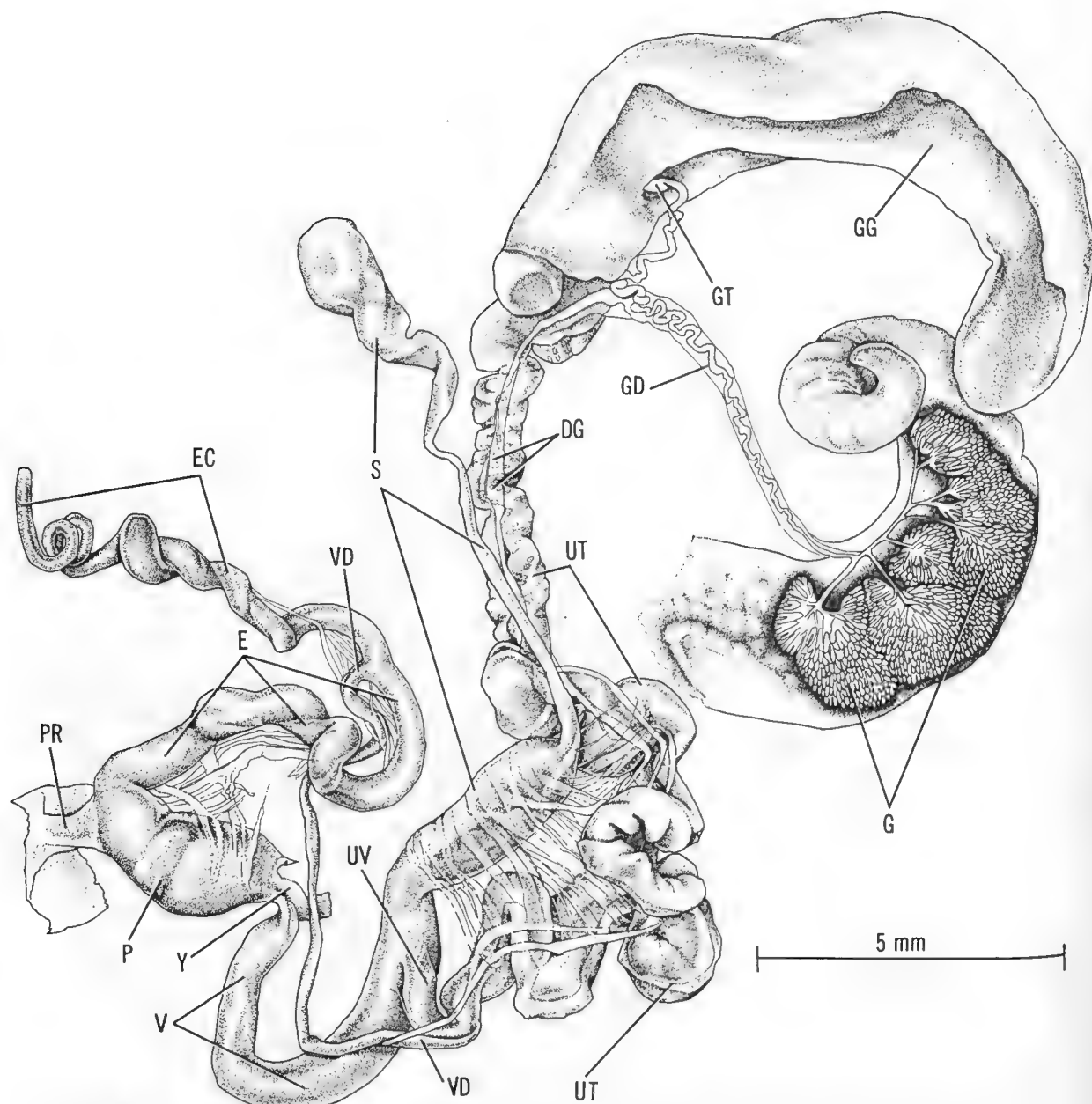


Fig. 20. Genitalia of *Amphidromus perversus* (Linné). On trees, Sanur, Bali, Indonesia, FMNH 198757. Collected by R.W. Skinner between 5-17 May 1977. Scale line equals 20 mm.

reduction of both the mesocone and the endocone. The tri-cuspid situation begins to be noticeable about 15 laterals outward and is a gradual shift. Outer marginals (Figs 6, 7, 13) are highly variable, may show splitting of all or no cusps, and have considerable individual variation in shape of the basal plate. The apparent differences illustrated for the three species are at least partly bridged by variation in other radulae studied, and should not be cited as indicative of species differences.

Jaw structure in *Amphidromus* (Figs 14, 15) compared with the average camaenid structure, shows reduction phenomena. The jaw is much thinner and less rigid, narrower, significantly elongated, and with greatly reduced vertical ribs. Haniel (1921: 40-45, figs 11, 12) illustrated the extreme variability in numbers of vertical

ribs within single populations. The jaw cannot be used for differentiating among species of *Amphidromus*.

Major Variations in the Genitalia

The few notes in early literature on the basic genital anatomy of *Amphidromus* are summarized by Laidlaw and Solem (1961: 516). For most of these, it is not possible to determine today which species was being studied. Haniel (1921: 57-68, figs 22-27) demonstrated considerable local variation in the length of the epiphallial caecum and in the external appearance of many genital features. He did not study the functioning surfaces of the genitalia. Haniel's outline drawings and poorly reproduced photographs make further analysis

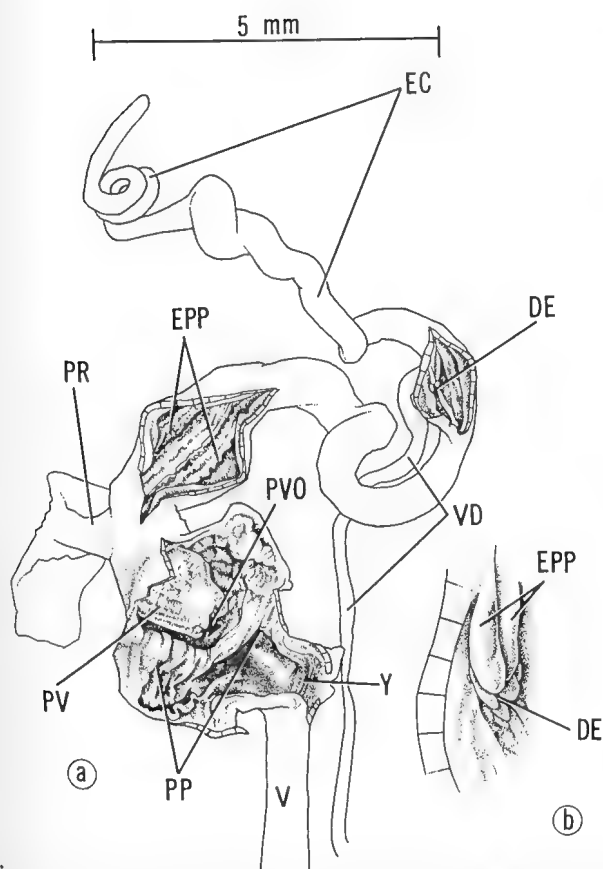


Fig. 21. Functioning surfaces of male terminal genitalia in *Amphidromus perversus* (Linné). On trees, Sanur, Bali, Indonesia, FMNH 198757. Scale line equals 10 mm. a, interior of penis chamber and epiphallus; b, detail of vas deferens opening into epiphallus.

of his data extremely difficult. Bishop (1977) found vergic differences among four Indonesian species and confirmed differences in lengths of the epiphallallic caecum, but presented no quantitative data and his simplified drawings are very difficult to interpret. Minato (1979) outlined the terminal genitalia of *A. poecilochrous jaeckeli*, but gave no internal details.

The three species reported on here are from widely separated localities, were collected in different seasons, are of different relative maturities, and were preserved in different ways, and initially a maximum of two individuals could be dissected for each. It is thus possible to present only preliminary notes and suggest lines of investigation. Even these limited data do, however, confirm the camaenid position of *Amphidromus* and show that the patterns of variation in the terminal male system exactly parallel patterns observed in West Indian species of *Pleurodonte* which are sympatric. This suggests that species recognition structural shifts also exist in *Amphidromus* and that study of the terminal genitalia functioning surfaces will permit ready determination of species limits. This will permit unravelling and organizing the bewildering shell colour variations that exist both allopatrically and sympatrically. A recent note on *A. perversus* by Skinner (1981) contained data suggesting that colour variations in the shells of *Amphidromus* may have the same type

of physiologically linked, ecological correlations that occur in the much more completely studied European *Cepaea*.

The genitalia of *A. perversus* (Figs 20, 21) show only a few unusual features for a camaenid. The mass of the ovotestis is tightly clumped, the hermaphroditic duct enters very near to the head of the talon (GT), there is a very tightly kinked lower portion of the prostate-uterus that is bound by fibres to the spermathecal shaft, and the epiphallallic caecum (EC) is very long. Laidlaw and Solem (1961: 520) point out that, in general, the epiphallallic caecum is elongated in members of *Amphidromus*, s.s., when compared with members of the subgenus *Syndromus*. This difference is confirmed by the conditions of *A. poecilochrous jaeckeli* (Fig. 23a), *A. cognatus* (Fig. 22a), and *A. porcellanus* (Bishop, 1977: 204, fig. 5f).

The penis of *A. perversus* is quite short, slightly bulbous, and has the walls (Fig. 21a) with vague spiral ridges. The verge (PV) is short, conic, with a very wide terminal pore (PVO). The epiphallus (E) has weak, slightly crenulated ridges basally that become smooth near the entrance of the vas deferens (VD), which is flanked (Fig. 21b) by a series of low, finger-like pilasters.

The dissected individuals of *Amphidromus poecilochrous jaeckeli* are 'new adults' with the characteristic minute albumen gland (GG, Fig. 22a), and extremely slender prostate-uterus area. The ovotestis is broken up into a series of distinct lobules, there is near-apical entrance of the hermaphroditic duct (GD) into the talon (GT), the spermatheca is quite slender for its entire length, and the epiphallallic caecum (EC) is quite short.

Amphidromus poecilochrous jaeckeli (Fig. 22b) has corrugated longitudinal pilasters lining the penis interior, the verge (PV) is grossly enlarged to a flattened tip with the pore (PVO) shifted to one side and located almost half-way toward the verge apex. Epiphallallic sculpture is less clearly developed and the pattern of ridges around the entrance of the vas deferens is simplified compared with that found in *A. perversus*.

In *A. cognatus* (Figs 23a-d, 24a, b), there is clear lateral entrance of the hermaphroditic duct onto the talon (Figs 23c, 24a), the ovotestis is also clearly divided into lobules (Figs 23b, 24b), and the epiphallallic caecum is quite short (EC). *A. cognatus* is unusual in having the vagina (Fig. 23a) folded over with connective tissue binding the folded area, whereas in *A. perversus* it is the lower prostate-uterus (Fig. 20) that is folded and bound to the spermathecal shaft. The immature genitalia of *A. poecilochrous jaeckeli* do not permit study of this region. The walls of the penis chamber in *A. cognatus* (Fig. 23d) are smooth, with vague longitudinal pilasters below. The verge is conical, with strongly wrinkled surface, slightly subterminal pore (Fig. 23e, PVO), and with epiphallallic pilasters lining the inner verge surface (Fig. 23e, EPP).

Specimens collected 11 November 1980 had the ovotestis enlarged (Fig. 24b) and the prostate-uterus (Fig. 24a) distinctly more swollen than in adult

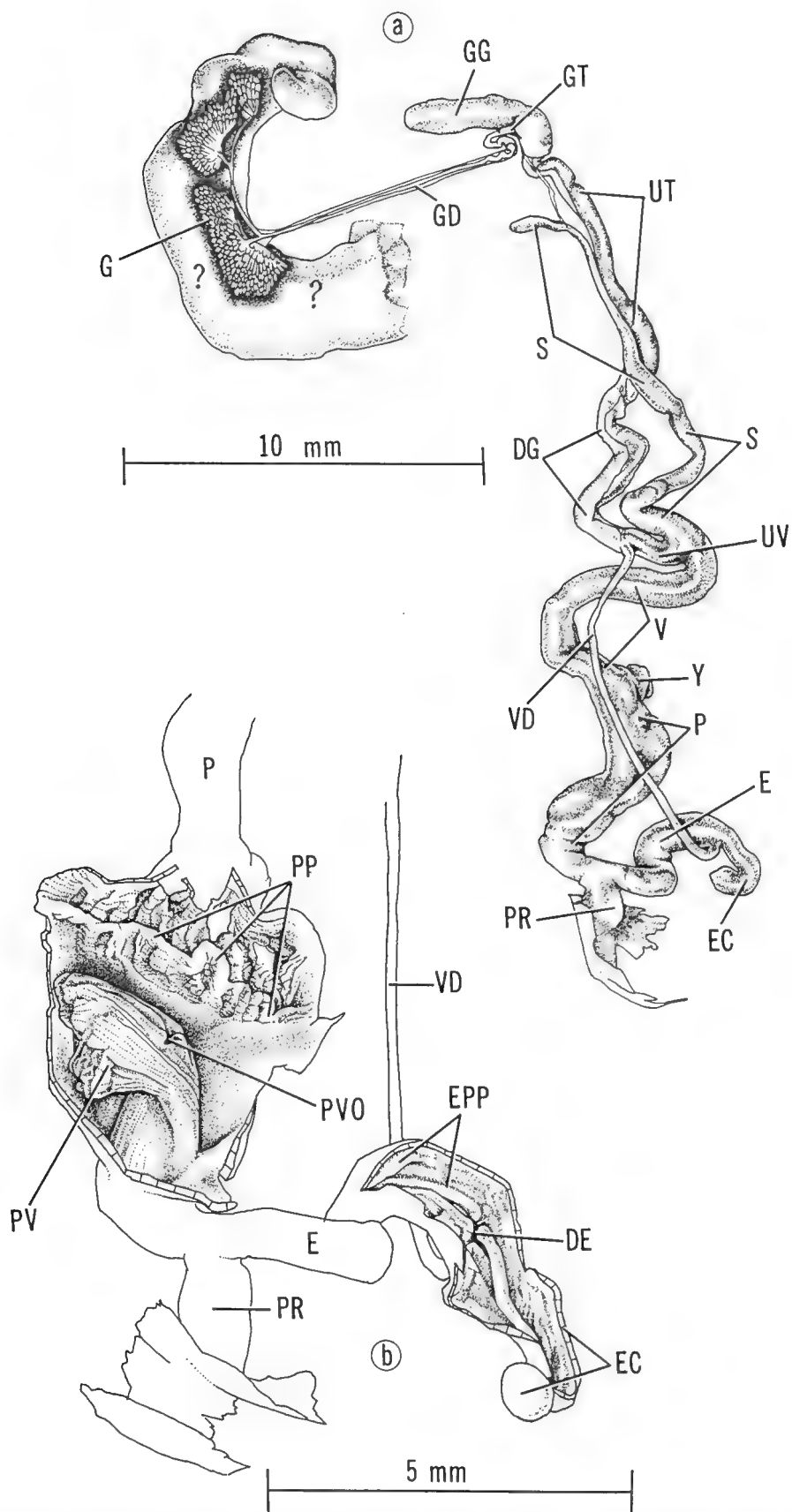


Fig. 22. Genitalia of *Amphidromus poecilochrous jaeckeli* Laidlaw. Jungle near Konga, Flores, Indonesia, FMNH 198758. Collected by R.W. Skinner in June 1975. Scale lines as marked. a, whole genitalia, male adult phase; b, interior of penis chamber and epiphallus.

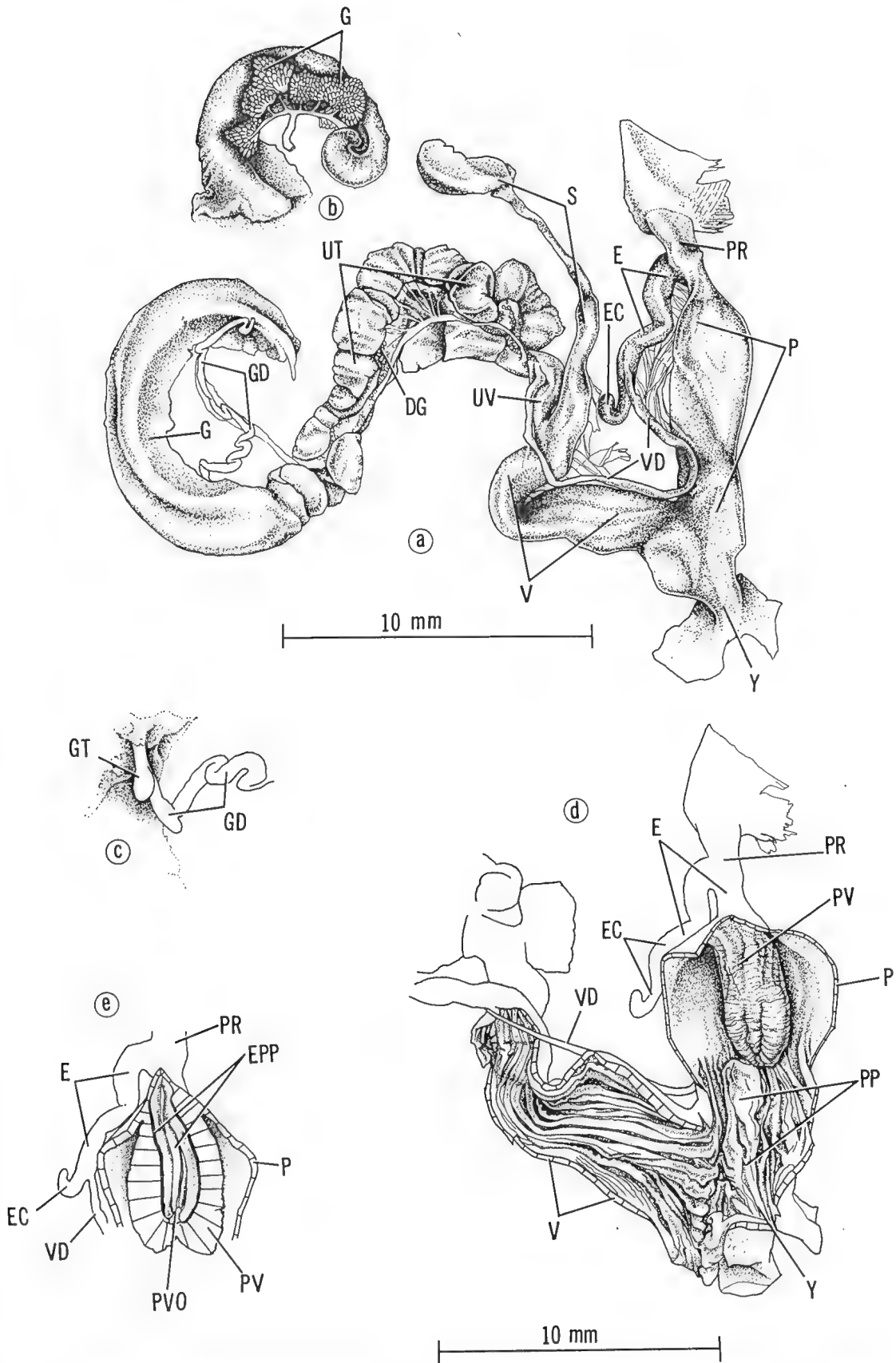


Fig. 23. Genitalia of *Amphidromus cognatus* Fulton. Along creek at bridge 3-4 km from Paru, Melville I., Northern Territory, Australia. AM C.121192. Collected by P.H. Colman and V. Kessner on 21 March 1980. Scale lines as marked. **a**, whole genitalia of fully mature individual; **b**, ootestis; **c**, detail of hermaphroditic duct-talon junction; **d**, interior of terminal genitalia.

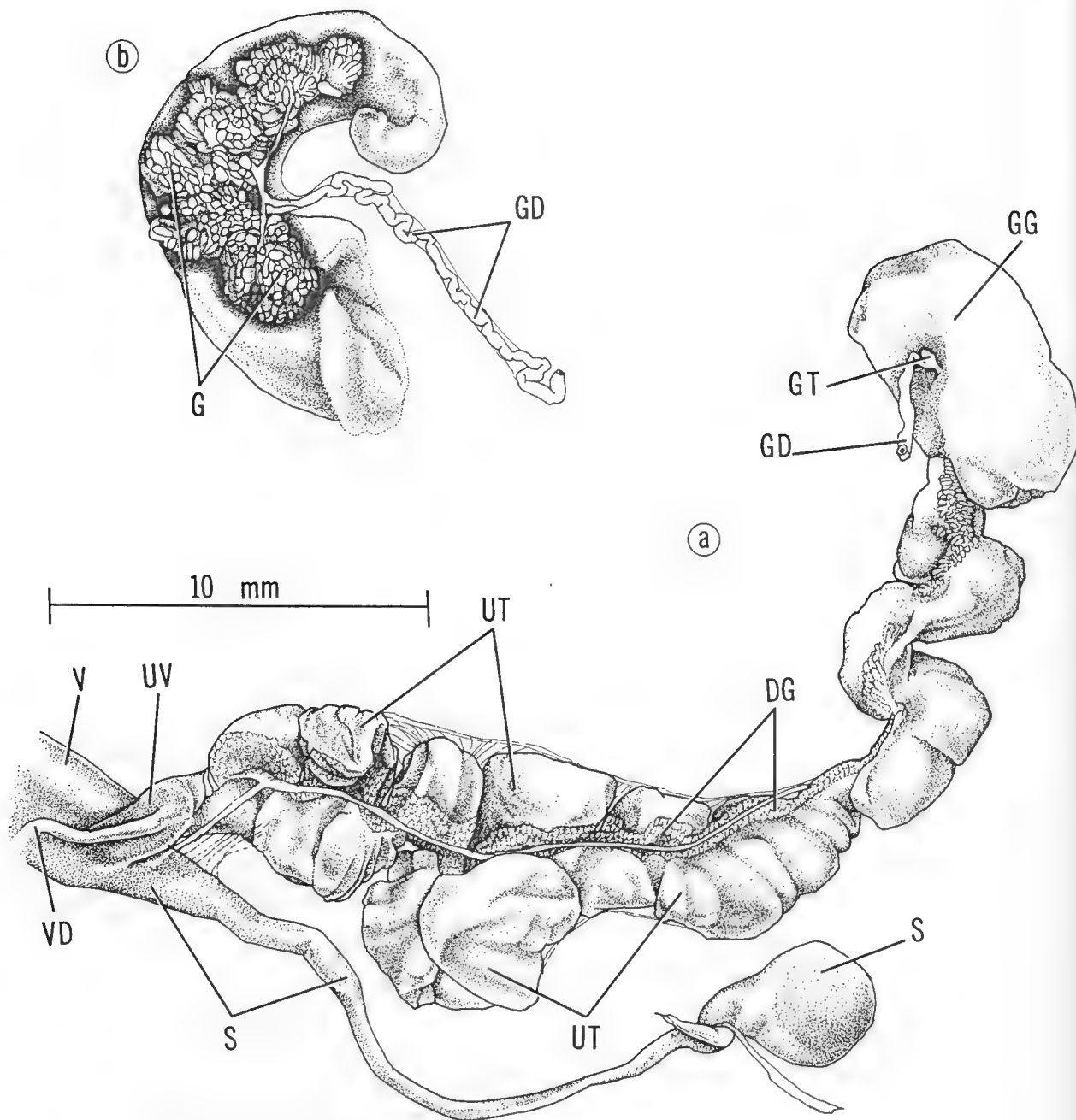


Fig. 24. Genital details of *Amphidromus cognatus* Fulton. Rain forest behind pumps, Milikapiti Bay, Melville I., near Darwin, Northern Territory, Australia, FMNH 198760. Collected by V. Kessner 11 November 1980. a, pallial and apical genitalia showing enlarged uterus, hermaphroditic duct; b, hermaphroditic gland.

specimens collected 21 March 1980. The former were from near the start of the wet season, the latter from near the late wet season. When the November specimens were received at the Australian Museum, about a dozen eggs were loose in the bottle. Dissecting four (of 15) adults was possible. One dissected individual had numerous calcium granules in the uterine walls, but none had eggs in the tract. It seems probable that during the drowning process, all encapsulated eggs would have been expelled, but we do not know how many eggs had been laid prior to collection.

Obvious differences among the species in regard to prostate-uterus length and development probably are mainly seasonal, since the specimens of *A. cognatus* were collected in March 1980, near the end of the wet season, but during a time of normal activity; those of *A. perversus* were taken in early to mid-May 1977, a time that approximates the normal start of dry season conditions; and those of *A. poecilochrous jaeckeli* were obtained in June 1975, during the dry season. The latter specimens were conchologically barely adult. The pattern of camaenids becoming male adult at the end

of one wet season, with the albumen gland and prostate-uterus areas remaining undeveloped until the middle or latter part of the following wet season, is typical for Australian genera, such as *Xanthomelon* and *Torresitrachia* (Solem, 1979), and *Amplirhagada* (Solem, 1981). Size and shape variations in these features thus have no systematic importance.

Changes in the point at which the hermaphroditic duct (GD) enters the talon (GT), length of the epiphallal caecum (EC), pattern of pilasters around the entrance of the vas deferens (VD) into the epiphallus (E), and details of vaginal (V) length, almost certainly will be useful in distinguishing species. The patterns of structural variation with the penis itself—smooth walls; spiral or longitudinal ridges that may be smooth or corrugated; verge shape variation from simple conical to elongate-oval to expanded tip; verge pore terminal, sublateral, or high lateral in position—are exactly the types of changes found in sympatric species of *Pleurodonte* on the island of Dominica, Lesser Antilles (Solem, in preparation). These changes are equivalent to the patterns for species recognition found in Australian camaenids (Solem, 1979, 1981 a, b, in press), and thus suggest that the general pattern for the Camaenidae is to use structures of the terminal genitalia for species recognition purposes. Such alterations can be on the functioning surfaces of the male and/or female terminalia (Solem, 1981 a, b). Bishop (1977) found shape differences in the verges of Javanese *Amphidromus*, but did not discuss or illustrate pore position and gave only rudimentary data on wall sculpture of the male system. Nevertheless, this confirms widespread variation patterns in the male system.

Gross Anatomy

Externally, the body of *Amphidromus* is without unusual features. The head warts that are characteristic of *Rhagada* and some of the Japanese camaenid taxa are absent. Body colour is monochrome.

Pallial structures are typically camaenid, with a narrow and quite elongated kidney that abuts solidly against the most anterior intestinal loop at the apex of the pallial cavity. Despite the altered whorl count and profile in comparison with typical camaenids, no detectable pallial reorganization was discovered. Further comments and illustrations will be presented elsewhere.

ACKNOWLEDGEMENTS. For making the material available for this study, I wish to thank Dr Winston Ponder and Mr Philip Colman, the Australian Museum, Sydney; Mrs Renate Wittig Skinner, Greenville, North Carolina; and Dr Peter Mordan, British Museum (Natural History), London. Illustrations of anatomy are by Linnea Lahlum, Illustrator, Division of Invertebrates, Field Museum of Natural History, and were prepared with support of National Science Foundation grant DEB 78-21444. The scanning electron microscope photographs were taken by the author on a Cambridge S4-10 Stereoscan, provided to Field Museum of Natural History by National Science Foundation grant BMS 72-02149. The assistance of Associate Dorothy Karall, who mounted and labelled all

illustrations; Ron Testa for shell photography; Margaret Baker, Custodian, Division of Invertebrates, for aspects of specimen handling and SEM preparation; and Mrs Valerie Connor-Jackson, formerly Secretary, Division of Invertebrates, for manuscript preparation aid, are very gratefully acknowledged.

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The New Zealand and South-east Australian Species of *Aora* Krøyer (Amphipoda, Gammaridea)

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ABSTRACT. Six species of *Aora* are reported from New Zealand and south-east Australia: *Aora typica* Krøyer, *A. maculata* (Thomson), *A. mortoni* (Haswell), *A. hebes* n.sp., *A. hircosa* n.sp., and *A. adpressa* n.sp. A key is given to the males of *Aora* species of the world.

MYERS, A.A., & P.G. MOORE, 1983. The New Zealand and south-east Australian species of *Aora* Krøyer (Amphipoda: Gammaridea). Records of the Australian Museum 35(4): 167-180.

The genus *Aora* Krøyer was first recorded in New Zealand waters by Thomson (1879), who erected the species *Microdeutopus maculatus* Thomson. In the same year, Haswell recorded the genus from Australian waters under the names *M. mortoni* Haswell and *M. tenuipes* Haswell. Apart from a further paper by Haswell (1882) in which these latter two species were redefined, no further work has been published on Australian species. In New Zealand, Chilton (1885) recorded the occurrence of two 'forms' of male *Aora*, but placed both as forms of *A. typica* Krøyer, a species originally described from Chile. Stebbing (1906) synonymized all the then known world *Aora* species with *A. typica* Krøyer, thereby stifling critical analysis of the genus for over half a century, although Schellenberg (1926) and K.H. Barnard (1932) both erected further 'forms' of *A. typica*. Myers (1969) and J.L. Barnard (1972) both suggested that the variously described 'forms' of *A. typica* warranted specific status, and fourteen species are now recognized in world seas. J.L. Barnard (1972) reported two species of *Aora* from New Zealand waters, but although he attributed one species to *A. maculata* (Thomson), he was unable to allocate the other to a known species, probably owing to his not having fully adult males of the latter species before him. It is clear from his excellent figures of a juvenile male that his latter species was referable to *A. typica* Krøyer.

We have had the opportunity to study several collections of *Aora* from New Zealand and Australia (including Tasmania) and have found six species to be present: *A. mortoni* (Haswell) (of which *M. tenuipes* Haswell represents the female), *A. typica* Krøyer, *A. maculata* (Thomson), *A. hircosa* n.sp., *A. hebes* n.sp., and *A. adpressa* n.sp.

In general, *Aora* species are morphologically very uniform except for the highly diagnostic male gnathopoda. During the course of the present work, the appendages (including the mouthparts) of all six species

were compared and numerous small differences were noted. However, material from a wider range of localities is required before the specific significance of these differences can be ascertained by more detailed morphometric analysis. Many of the differences observable are apparently correlated with size, so that the appendages of small species agree closely in morphology with the corresponding appendages of small specimens of larger species. It is premature to attempt to compare the detailed morphology of the various species but we feel that a valuable contribution can be made by establishing the presence of at least six species in the region, elucidating the synonymy of previously recorded *Aora* material, and facilitating the identification, at least of males, of the New Zealand and SE Australian species. To this end, the paper concentrates on the morphology of the highly diagnostic male gnathopoda, although female gnathopoda and selected mouthparts are also figured, as are lateral views of entire male specimens.

In live material, colour patterns will almost certainly be of great value in segregating the species. Where known, the colour pattern of living material is described, otherwise the pattern observed in preserved material is given. The reader should be aware that because of differential fading of pigments in the pattern mosaic, preserved material may appear very different from live material.

A key to the males of all world species of *Aora* is provided.

Some of the material on which this study is based was collected by one of us (A.A.M.) but the greater part was made available to us by the generosity of Ms M. Drummond, National Museum of Victoria (NMV), Dr J.K. Lowry, Australian Museum (AM), Mr T.M. Walker and Mr G. Edgar, University of Tasmania (UT) and Prof. S. Ruffo, Museo Civico di Storia Naturale, Verona (VM).

Key to Aora Spp. (Males Only) of the World

1. Gnathopod 2 entire anterior margin of carpus and propodus densely clothed in long setae 2.
- Gnathopod 2 anterior margin of carpus and propodus weakly setiferous; if long setae present, then restricted to distal portion on either carpus or propodus 4.
2. Coxa 2 subtriangular *A. hebes* n.sp.
- Coxa 2 not subtriangular 3.
3. Gnathopod 1 propodus very short, $< \frac{1}{2}$ carpus *A. inflata* Griffiths, 1976
- Gnathopod 1 propodus elongate, $> \frac{2}{3}$ carpus *A. murtoni* (Haswell, 1879)
4. Gnathopod 1 carpus with postero-distal tooth *A. gibbula* Barnard, 1932
- Gnathopod 1 carpus without postero-distal tooth 5.
5. Gnathopod 1 basis with postero-distal 'brush' of long setae *A. trichobostrychus* Stebbing, 1888
- Gnathopod 1 basis without postero-distal 'brush' of long setae 6.
6. Gnathopod 1 basis anterior margin with triangular tooth, antero-distal margin with rounded flange, ischium anterior margin with rounded flange *A. typica* Krøyer, 1845
- Gnathopod 1 basis and ischium not as above 7.
7. Gnathopod 1 merus densely setose 8.
- Gnathopod 1 merus weakly setiferous 9.
8. Gnathopod 1 propodus anterior margin with very long setae .. *A. atlantidea* Reid, 1951
- Gnathopod 1 propodus anterior margin with setae of only moderate length *A. hircosa* n.sp.
9. Gnathopod 1 basis with crenulate antero-proximal process *A. anomala* Schellenberg 1926
- Gnathopod 1 basis without crenulate antero-proximal process 10.
10. Gnathopod 2 basis anterior margin markedly convex. Pereopod 6 basis postero-distal margin produced into 'heel' *A. gracilis* (Bate, 1857)
- Gnathopod 2 basis anterior margin straight or concave. Pereopod 6 basis postero-distal margin without 'heel' 11.
11. Gnathopod 2 carpus elongate, nearly parallel-sided, almost twice length of propodus *A. adpressa* n.sp.
- Gnathopod 2 carpus triangular, equal to or a little longer than propodus 12.
12. Gnathopod 2 propodus short, anterior margin strongly convex *A. spinicornis* Afonso, 1976
- Gnathopod 2 propodus equal in length to carpus, propodus anterior margin weakly convex 13.
13. Antenna 2 strongly setose *A. maculata* (Thomson, 1879)
- Antenna 2 weakly setiferous *A. kergueleni* Stebbing, 1888

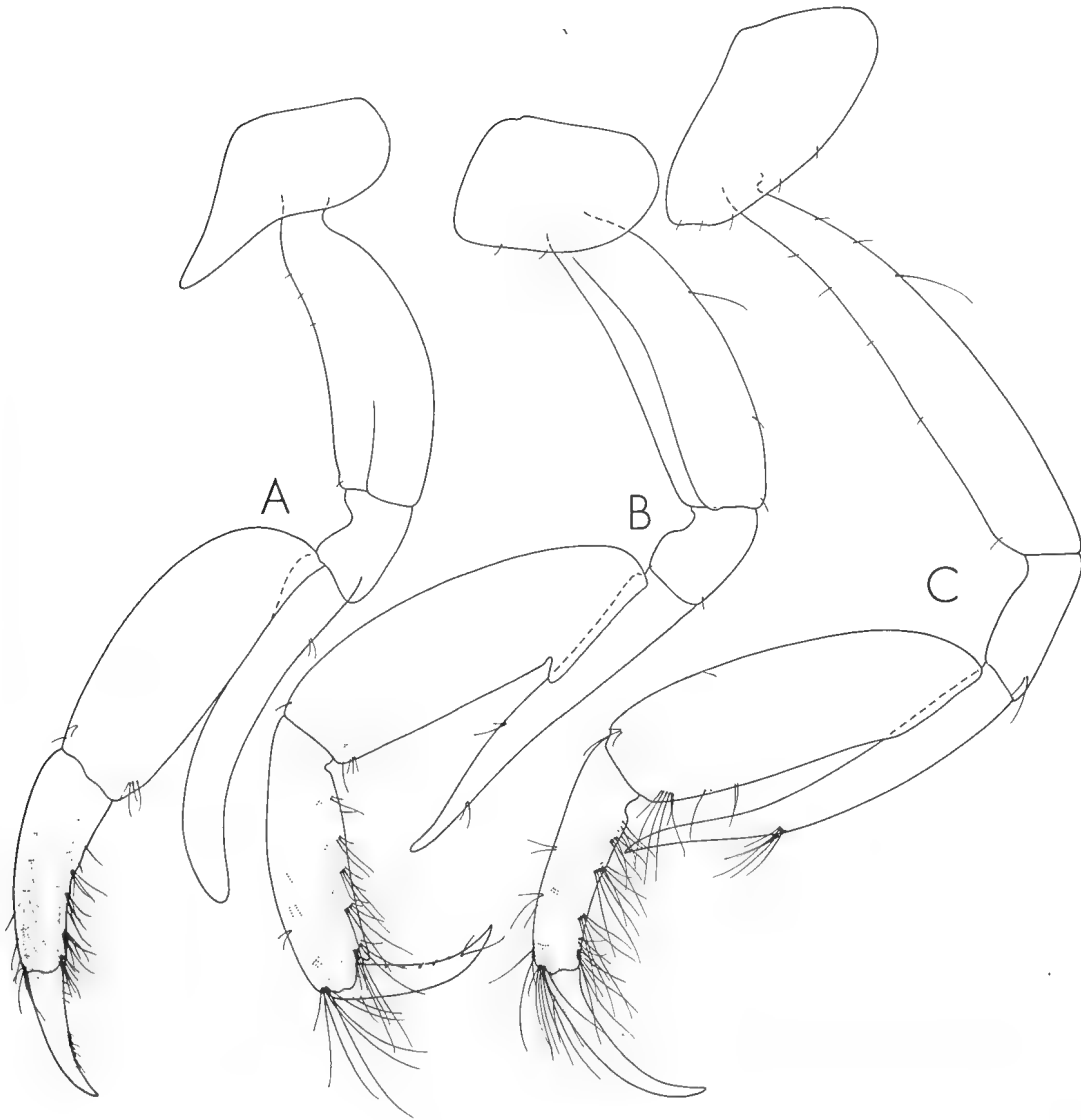


Fig. 1. Hyperadult ♂ gnathopod 1 of A, *A. hebes* (Sydney Harbour); B, *A. mortoni* (Western Port); C, *A. maculata* (Tinderbox).

***Aora typica* Krøyer, 1845**

Figs 2, 3, 4, 13

Aora typica Kroyer, 1845, p. 238, pl. 3, fig. 3.—Della Valle, 1893, p. 409, pl. 56, figs 38-40; Chilton, 1909, p. 645; Ledoyer, 1967, p. 131, fig. 15; Myers 1973, p. 287, fig. 14. *Aora typica* 'form 1' Chilton, 1885, p. 370. *Aora typica* 'form *typica*' Stephensen, 1949, p. 41, fig. 18. *Aora* sp. Barnard, 1972, p. 124, fig. 10 i-j. *Lalaria longitarsus* Nicolet, 1849, p. 243, pl. 2, fig. 8 a-f.

Type locality: Valparaiso, Chile.

Material examined: 37♂ 46♀ immature, Snares Island (AM); 2♀ 13 immature, Kaikoura (AM); 5♂ 6♀, Lyttelton (VM); 3♂ 14♀, Dunedin (NMV); 1♂, Port Jackson (Sydney Harbour) (AM).

Diagnosis. Maximum length 12.0 mm. Male pereon segments lacking sternal processes. Male gnathopod 1 coxa with anterodistal corner strongly produced, very

acute; basis anterior margin with strong, medial, triangular process and large flap-like distal process; ischium anterior margin with large, rounded, 'wing'; merus shorter than carpus, acute; propodus more than two-thirds length of carpus; dactylus swollen medially. Male gnathopod 2 small, only moderately setose; palm of propodus very oblique. Female gnathopod 1 propodus with palm distinctly excavate.

Colour in life uniformly pinkish without markings (J.K. Lowry, pers. comm.); in alcohol, whitish.

Discussion. The peculiar 'wings' on the basis and ischium, and the triangular anterior marginal process of the male gnathopod 1 immediately distinguish adult and sub-adult males from all other *Aora* species.

World distribution. This species is widely distributed in the Southern Hemisphere between latitudes 20°S and 50°S. However, it is apparently replaced in Tierra del Fuego by *A. anomala* Schellenberg and in South Africa by *A. gibbula* Barnard, *A. anomala*

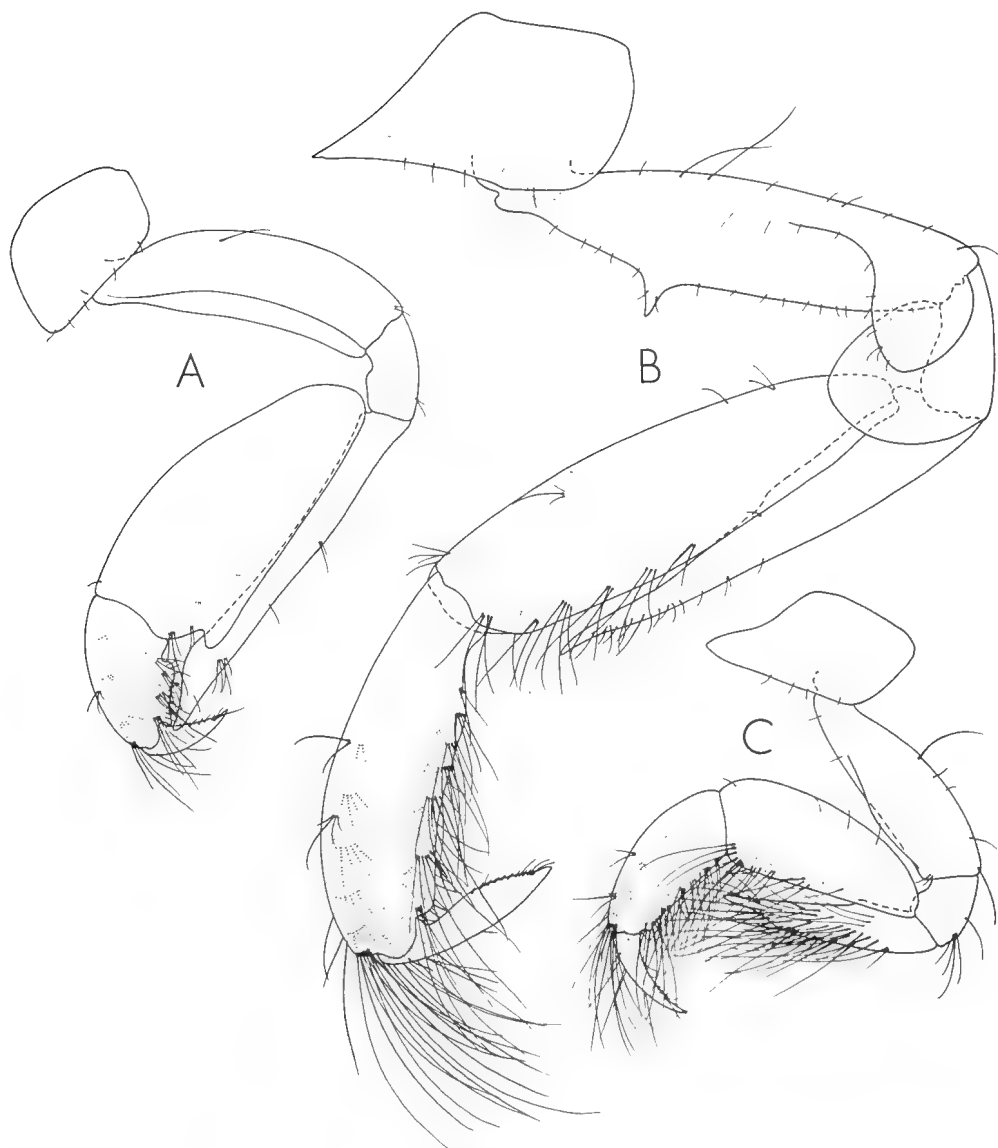


Fig. 2. Hyperadult ♂ gnathopod 1 of A, *A. adpressa* (Western Port); B, *A. typica* (Snares Islands); C, *A. hircosa* (Tinderbox).

Schellenberg, *A. inflata* Griffiths and, according to Griffiths (1975), *A. kergueleni* Stebbing. At Kerguelen Island, two species, *A. kergueleni* and *A. trichobostrius* Stebbing, are known.

Confirmed records of *A. typica* sensu stricto are Chile (Krøyer, 1845; Nicolet, 1849) Tristan da Cunha, Nightingale, Inaccessible (Stephensen, 1949) New Zealand south to the Snares Islands (Chilton, 1885, 1909, and herein), Madagascar (Ledoyer, 1967) and Sydney, Australia (herein).

Aora maculata (Thomson, 1879)

Figs 1, 5, 6, 13

Microdeutopus maculatus Thomson, 1879, p. 331, pl. 16, figs 5-8.

Microdentopus [sic] *maculatus*.—Thomson, 1880, p. 217, fig. 7 a-c; Chilton, 1882, p. 173, pl. 8, fig. 3a, b.

Aora typica—Thomson, 1879, p. 331; Thomson, 1880, p. 216;

Thomson & Chilton, 1886, p. 147; Thomson, 1889, p. 261; Hutton, 1904, p. 260; Thomson 1913, p. 245.

Aora maculata.—Barnard, 1972, p. 124, fig. 10 f-h; Lowry, 1974, p. 102, 122, fig. 5a.

N.B. The records of Chilton 1909, and of Stephensen, 1927, 1938 (see Lowry, 1976, p. 26) cannot with certainty be attributed to this species.

Type locality. Dunedin, New Zealand.

Material examined. 32♂ 151♀ 79 imm., Snares Island (AM); 2♂ 1♀, Auckland Islands (AM); 21♂ 37♀ 18 imm., Tinderbox, SE Tasmania in algae (UT); 25♂ 23♀, Western Port, Victoria (NMV); 15♂ 32♀ 10 imm., Kiama, N.S.W., in *Hormosira*, intertidal (AAM); 2♂ 12♀ 5 imm., Sydney Harbour, in *Pterocladia*, intertidal (AAM); 6♂ 7♀, Coogee, N.S.W. (AM); 4♂ 3♀ 2 imm., Merimbula, N.S.W. (AM & NMV); 1♂ 1♀, Jiguma, N.S.W. (NMV).

Diagnosis. Maximum length 10.0 mm. Malc pereopod segments lacking sternal processes. Male gnathopod 1 coxa much deeper than broad, narrowing distally in

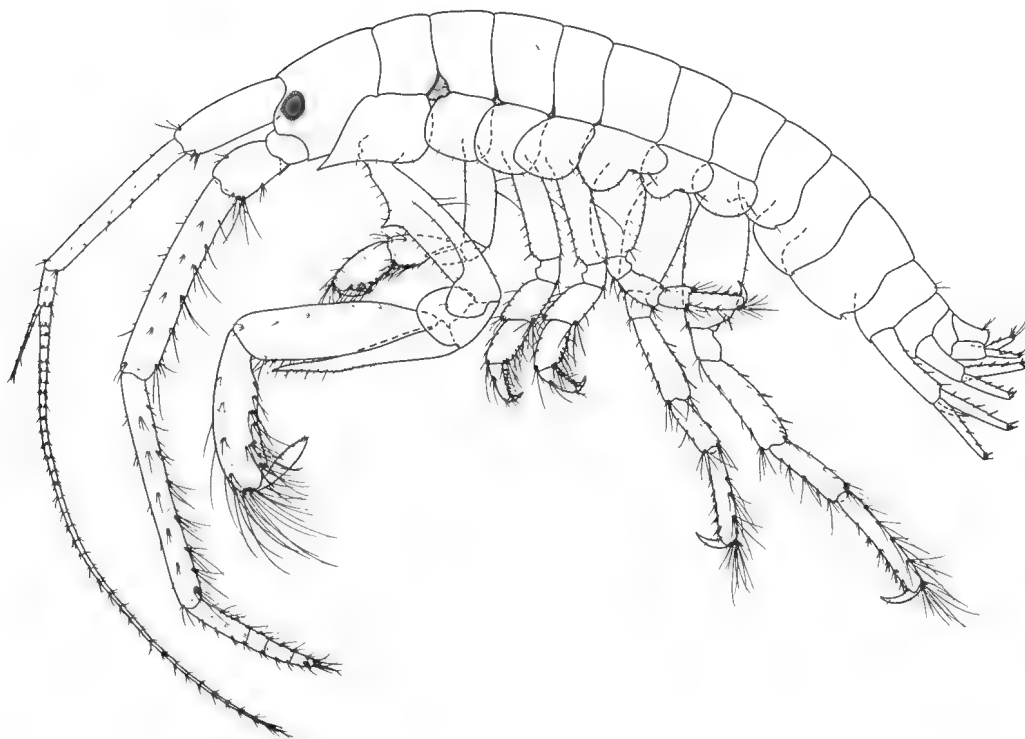


Fig. 3. ♂ *A. typica*, Snares Islands, lateral view.

hyperadults; broader than deep, the anterodistal corner produced, subacute in subadults (Fig. 5B); basis extremely elongate and slender in hyperadults, moderately slender in subadults; ischium elongate; merus longer than and weakly divergent from carpus; propodus little over half length of carpus; dactylus elongate, slender, curved, almost equal in length to propodus. Male gnathopod 2 small, only moderately setose, palm oblique. Female gnathopod 1 propodus subovoid, palm weakly excavate.

Colour in life, tan with discrete black spots; in alcohol white with black spots.

Discussion. This species resembles *A. kergueleni* Stebbing, but in that species the male gnathopod 1 merus is stout and shorter than the carpus, and the dactylus is distinctly serrate, while gnathopod 2 has a swollen palmar region. It also resembles *A. spinicornis* Afonso from which it differs in having the merus of gnathopod 1 extending beyond the end of the carpus and in lacking an inflated gnathopod 2 propodus. Hyperadult male *A. maculata* differ from all known *Aora* spp. in the shape of coxa 1.

World distribution. New Zealand including sub-Antarctic islands, Tasmania and SE Australia.

Aora mortoni (Haswell, 1879)

Figs 1, 7, 8, 13

Microdeuteropus [sic] *mortoni* Haswell, 1879, p. 339, pl. 22, fig. 2.—Chilton, 1884, p. 1040.

Microdeuteropus tenuipes Haswell, 1879, p. 339, pl. 22, fig. 1.—Chilton, 1884, p. 1040.

Microdeuteropus mortoni.—Haswell, 1882, p. 264.

Microdeuteropus tenuipes.—Haswell, 1882, p. 264.

Type locality. Sydney Harbour.

Material examined. 113♂ 138♀ 25 imm., Western Port, Victoria (NMV); 33♂ 68♀ 5 imm., Tinderbox, SE Tasmania in algae (UT); 15♂ 37♀, Sydney Harbour (including ♂ HOLOTYPE *M. mortoni* and ♀ SYNTYPES *M. tenuipes*) (AM).

Diagnosis. Maximum length 8.0 mm. Male pereon segments 2-3 with forward curved, slender, acute, sternal processes. Male gnathopod 1 coxa subrectangular, antero-distal corner unproduced, rounded; basis and ischium stout; merus almost straight, acute, diverging strongly from carpus distally; propodus three-quarters length of carpus, palm in hyperadults produced into a weak tooth; dactylus slender, two-thirds length of propodus. Male gnathopod 2 carpus and propodus anterior margin densely setose, palm oblique. Female gnathopod 1 propodus slender, palm distally excavate.

Colour in alcohol, whitish with brownish blotches on pereon, a particularly strong blotch on dorsum of segment 7. Head with reticulate pattern on dorsal surface.

Discussion. Only two other known world species of *Aora* have the greater length of the margins of both carpus and propodus of male gnathopod 2 densely setose, viz. *A. hebes* and *A. inflata*. *Aora mortoni* is readily distinguished from both by the structure of the male gnathopod 1, notably the unproduced coxa and divergent but almost straight, acute merus. In addition, this species and *A. adpressa* n.sp. are the only *Aora* spp.

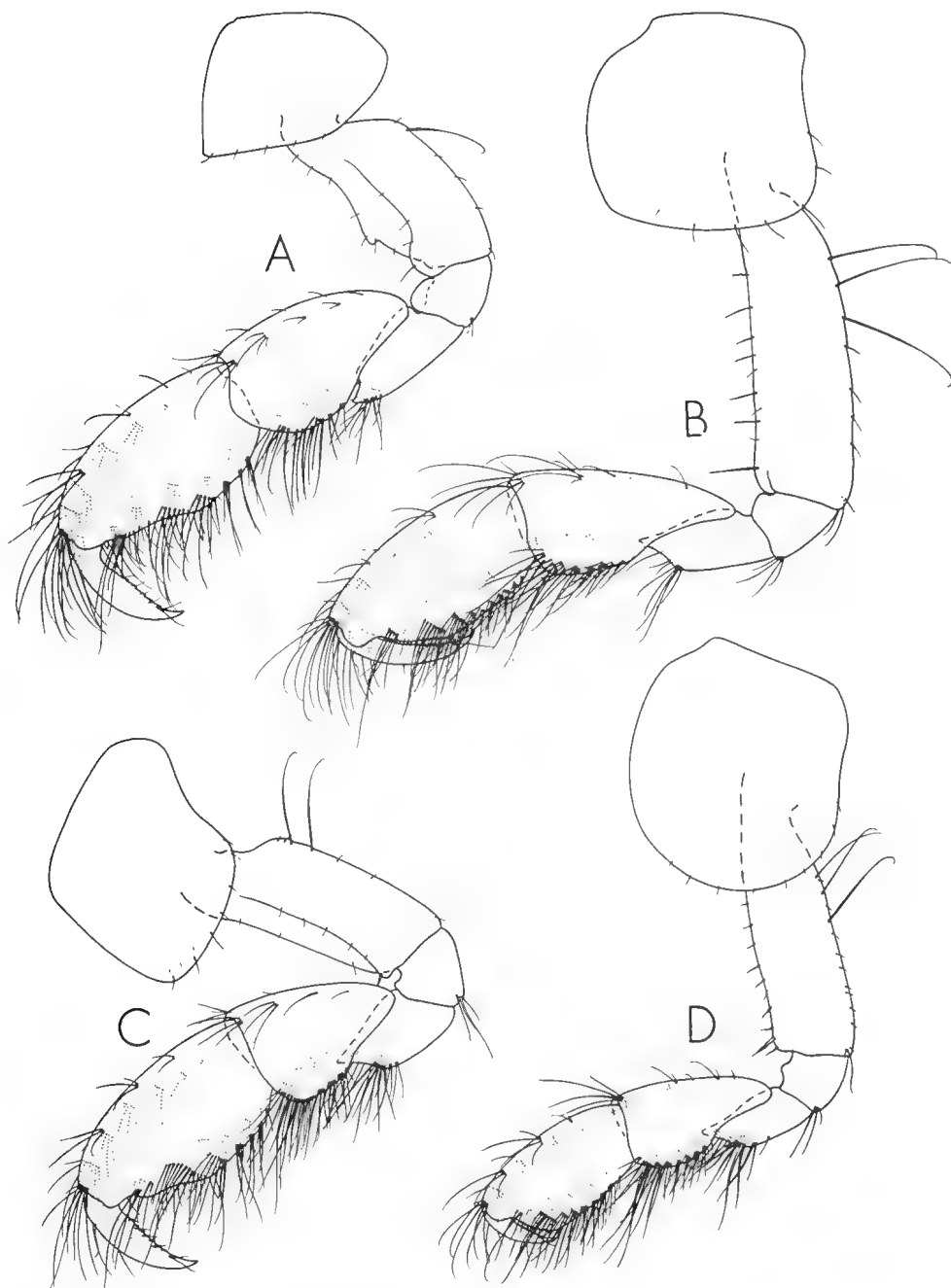


Fig.4. *A. typica*, Snares Islands. A, Subadult ♂ gnathopod 1; B, hyperadult ♂ gnathopod 2; C, ovigerous ♀ gnathopod 1; D, ovigerous ♀ gnathopod 2.

known to possess sternal pereon processes in the male, although some species may not have been examined for this character.

World distribution. Tasmania to Sydney.

***Aora hebes* n.sp.**

Figs 1, 9, 10, 13

Type material. HOLOTYPE ♂ 6.5 mm. East of North Head, Sydney, N.S.W. 33° 49'S, 151° 18'E, 21 m, in association with the sponge *Polymastrea cratica* February 1973, AM 22411. PARATYPES 18♂ 19♀ 4 imm., same locality and

date, in association with *P. cratica* and *Teichonella labyrinthica*, 19.8-25.9 mm, AM 22411.

Etymology. The name refers to the blunt end of the merus in hyperadult males.

Diagnosis. Maximum length 6.5 mm. Male pereon segments lacking sternal processes. Male gnathopod 1 coxa with anteroventral corner very strongly produced, acute; basis and ischium stout, merus swollen basally and then of almost equal diameter throughout its length, longer than carpus, strongly diverging distally, ending obtusely in hyperadults, acutely in subadults; propodus

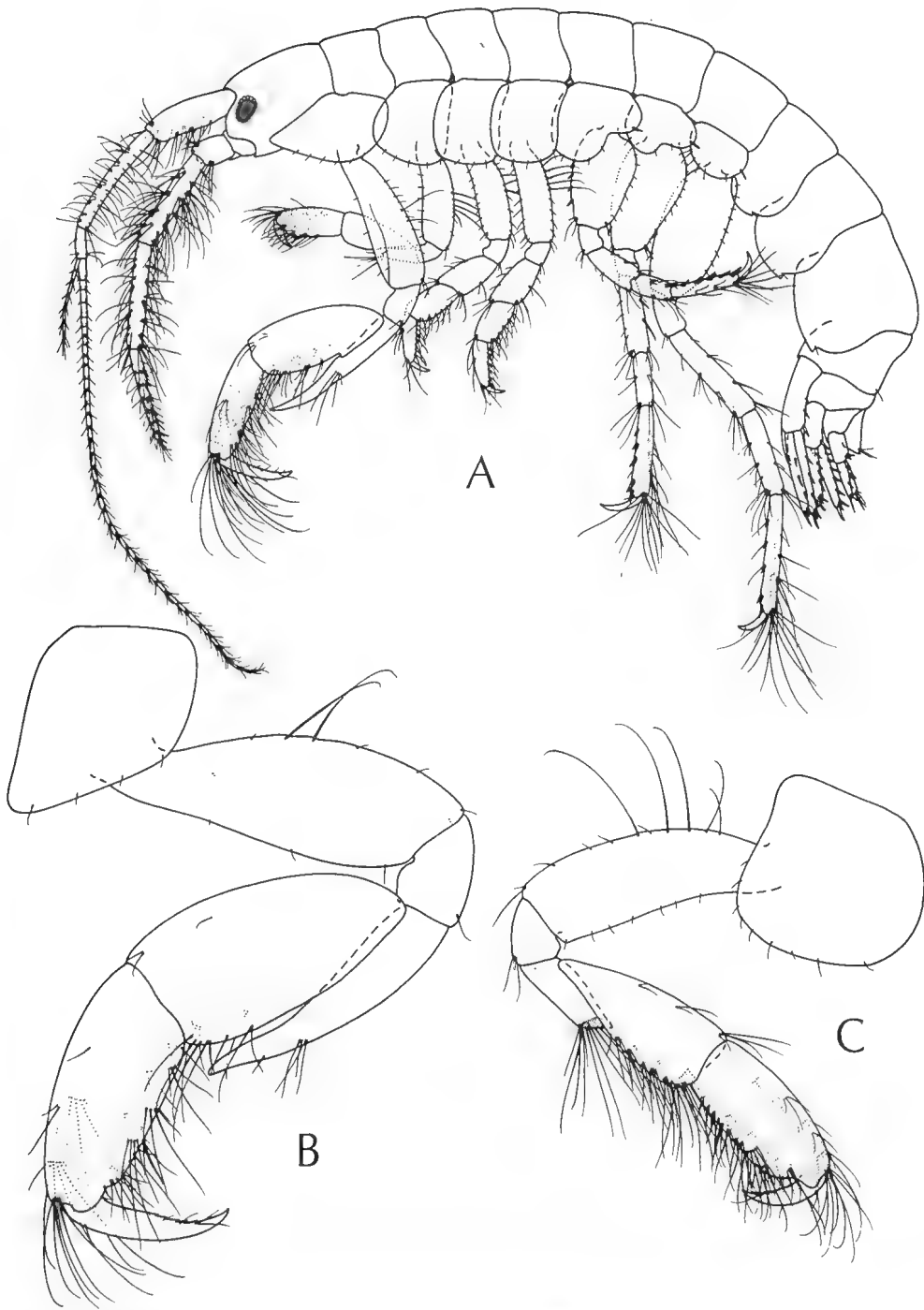


Fig. 5. ♂ *A. maculata*, Snares Islands. A, lateral view; B, subadult gnathopod 1; C, hyperadult gnathopod 2.

about two-thirds length of carpus; dactylus stout, about two-thirds length of propodus. Male gnathopods 2 carpus and propodus with anterior margin densely setose, palm oblique. Female gnathopod 1 propodus with distinct but short palm.

Description. Head ocular lobes moderately produced, obtuse; eye subround. Antenna 1 two-thirds body length, peduncular articles in the ratio 9:10:3, flagellum longer than peduncle with 19 articles; accessory flagellum with 4 articles, the terminal article

rudimentary. Antenna 2 less than two-thirds length of antenna 1, peduncular articles 4 and 5 subequal, flagellum shorter than peduncular article 5 with 8 articles. Male gnathopod 2 coxa subtriangular, deeper than broad, carpus elongate, propodus two-thirds length of carpus, palm oblique; dactylus fitting palm. Pereopods 3-4 coxae deep, dactylus almost half length of propodus. Pereopods 5-7 in length ratios 4:4:5, coxa 5 with deep anterior lobe. Epimera 2-3 with small posterodistal tooth. Uropod 1 peduncle with strong

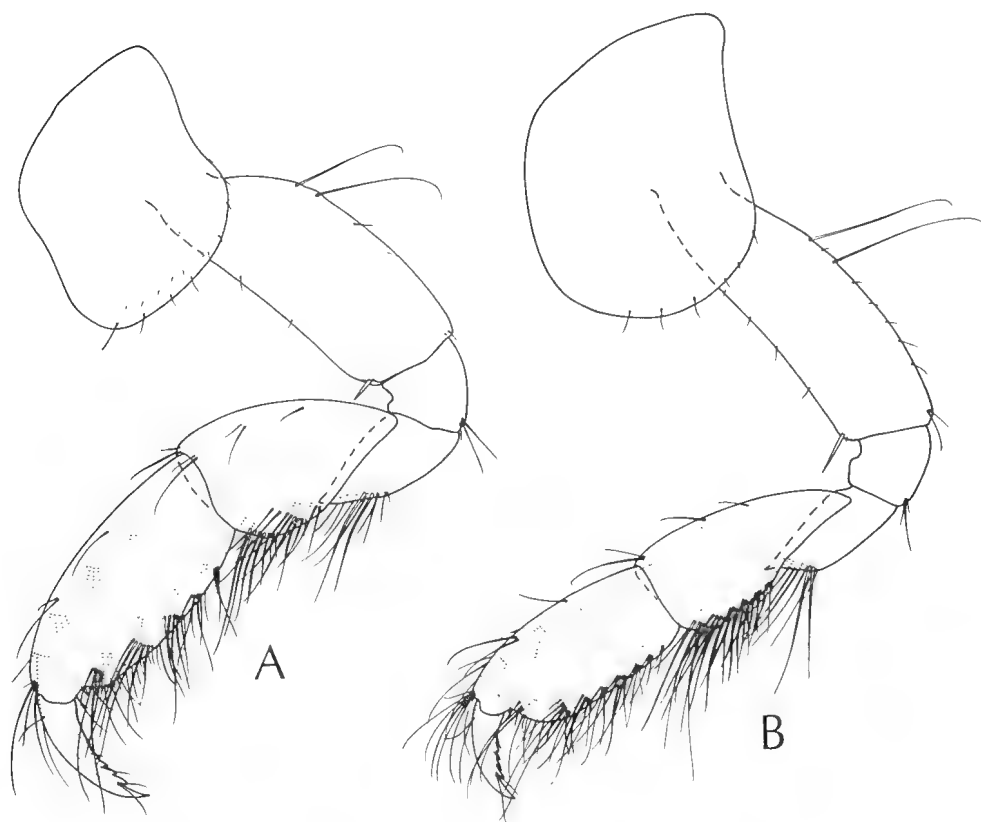


Fig. 6. Ovigerous ♀ *A. maculata*, Snares Islands. A, gnathopod 1; B, gnathopod 2.

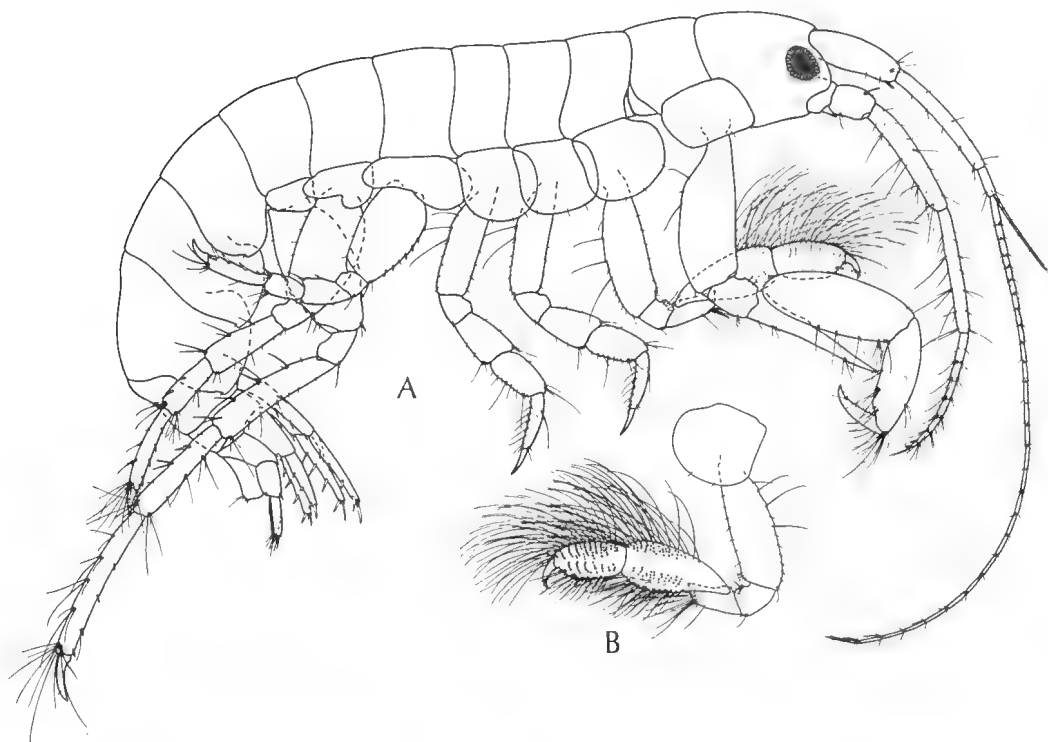


Fig. 7. ♀ *A. mortoni*, Western Port. A, lateral view; B, hyperadult gnathopod 2.

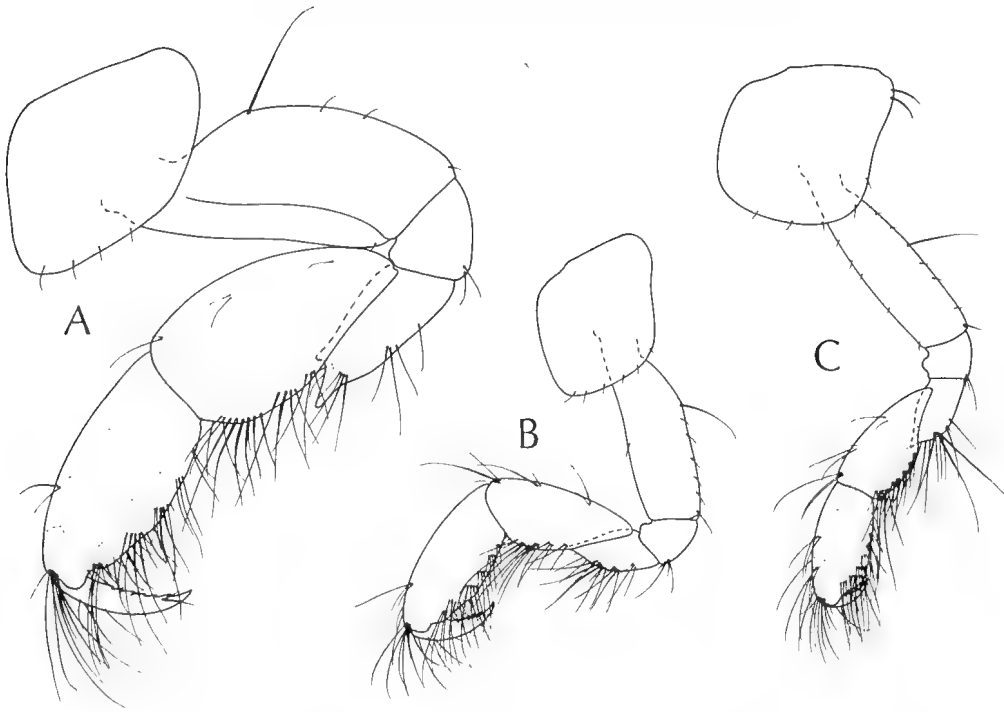


Fig. 8. *A. mortoni*, Western Port. A, subadult ♂ gnathopod 1; B, ovigerous ♀ gnathopod 1; C, ovigerous ♀ gnathopod 2.

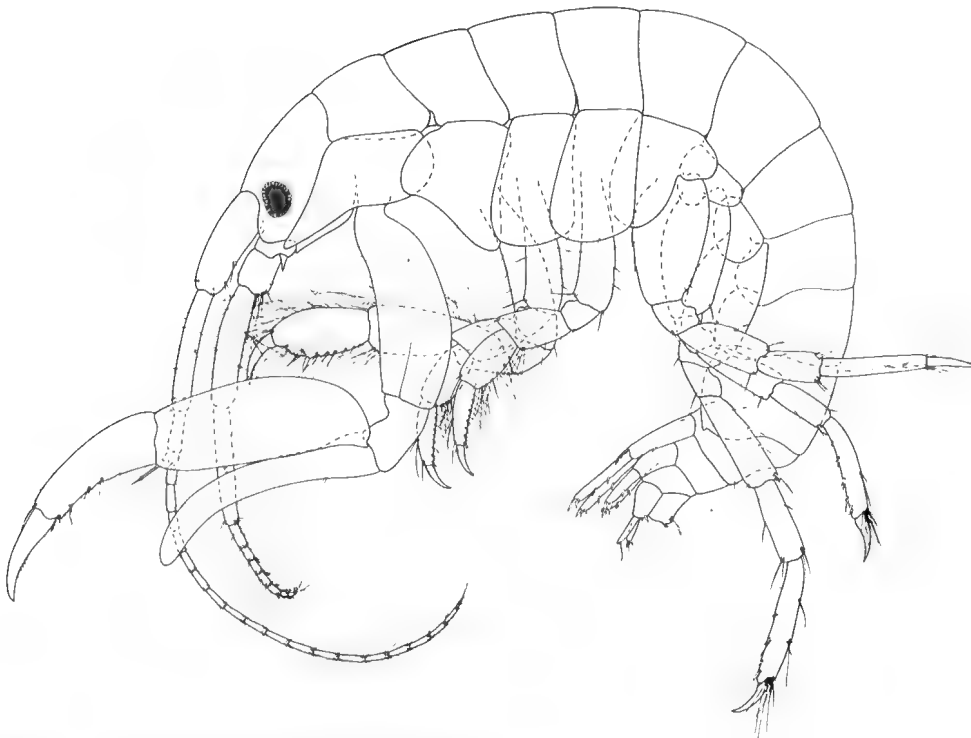


Fig. 9. ♂ *A. hebes*, Sydney Harbour, lateral view.

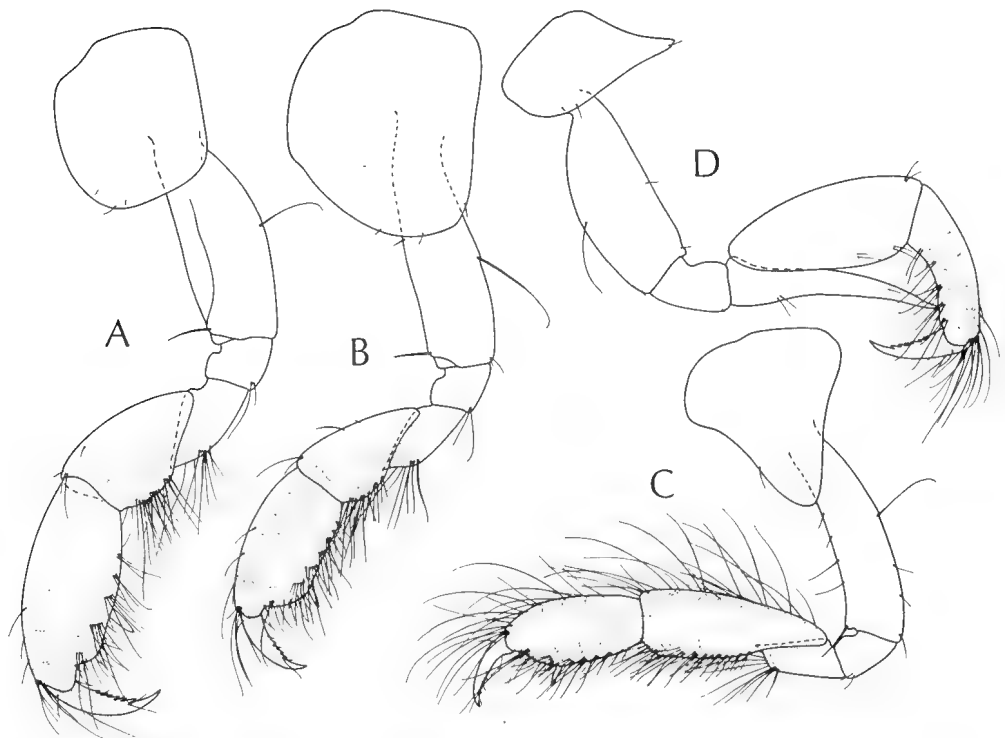


Fig. 10. *A. hebes*, Sydney Harbour. A, ovigerous ♀ gnathopod 1; B, ovigerous ♀ gnathopod 2; C, hyperadult ♂ gnathopod 2; D, subadult ♂ gnathopod 1.

interramal spiniform process. Uropod 2 peduncle lacking an interramal process. Uropod 3 rami subequal, lacking marginal spines, outer ramus with small second article.

Colour in alcohol, pale tan with numerous small reddish-brown spots.

Discussion. The peculiar blunt merus of the male gnathopod 1, the triangular coxa 2 of the male, and the deep coxae 3-5 of the male are unique among known world species of *Aora*.

World distribution. So far known only from Sydney Harbour but possibly overlooked elsewhere owing to its inquilinous habits.

Aora hircosa n.sp.

Figs 2, 12, 13

Type material. HOLOTYPE: 1♂ 6.0 mm. Tinderbox, south-east Tasmania in marine algae, T.M. Walker, 1977: NMV J1324. PARATYPES: 7♂ 18♀ 1 imm. Same data as holotype.

Other material. 4♂ 9♀, Fancy Point, SE Tasmania in algae, 2-3 m (UT); 4♂ 8♀ 2 imm., Western Port, Victoria (NMV).

Diagnosis. Maximum length 6.0 mm. Male pereon segments lacking sternal processes. Male gnathopod 1 coxa with anteroventral corner strongly produced, acute; basis and ischium stout; merus stout, strongly setose, narrow distally, acute, moderately divergent from and reaching end of carpus; carpus and propodus

stout, strongly setose on posterior margin, propodus over three-quarters length of carpus with stout palmar defining spine; dactylus over half length of propodus. Male gnathopod 2 of moderate size, only moderately setose, palm oblique. Female gnathopod 1 propodus with stout but distinct palm.

Description. Head ocular lobes moderately produced, obtuse; eye subround. Antenna 1 two-thirds body length, peduncular articles in the ratios 5:6:2, flagellum longer than peduncle, with 18 articles; accessory flagellum with 4 articles, the terminal article rudimentary. Antenna 2 over half length of antenna 1, peduncular articles 4 and 5 subequal, flagellum a little shorter than peduncular article 5, with 5 articles. Male gnathopod 2 slender, carpus a little longer than propodus, dactylus fitting palm. Pereopods 3-4 dactylus less than half length of propodus. Pereopod 5 normal, pereopods 6-7 unknown. Epimera 1-3 rounded, epimera 2-3 with small posterodistal tooth. Uropod 1 peduncle with strong interramal spiniform process. Uropod 2 peduncle with short, triangular, interramal process. Uropod 3 rami stout, subequal, outer ramus with small second article. Colour in alcohol pale cream with numerous small blackish-brown spots, which tend on the dorsum to form distinct, though weak, bands.

Discussion. The strongly setose merus of the male gnathopod 1 is found in only one other species, *A. atlantidea* Reid. This latter species differs from *A. hircosa* in the presence of very long setae on the anterior margin of the propodus of the male gnathopod 1. In addition, the merus of gnathopod 1 of male *A. hircosa*

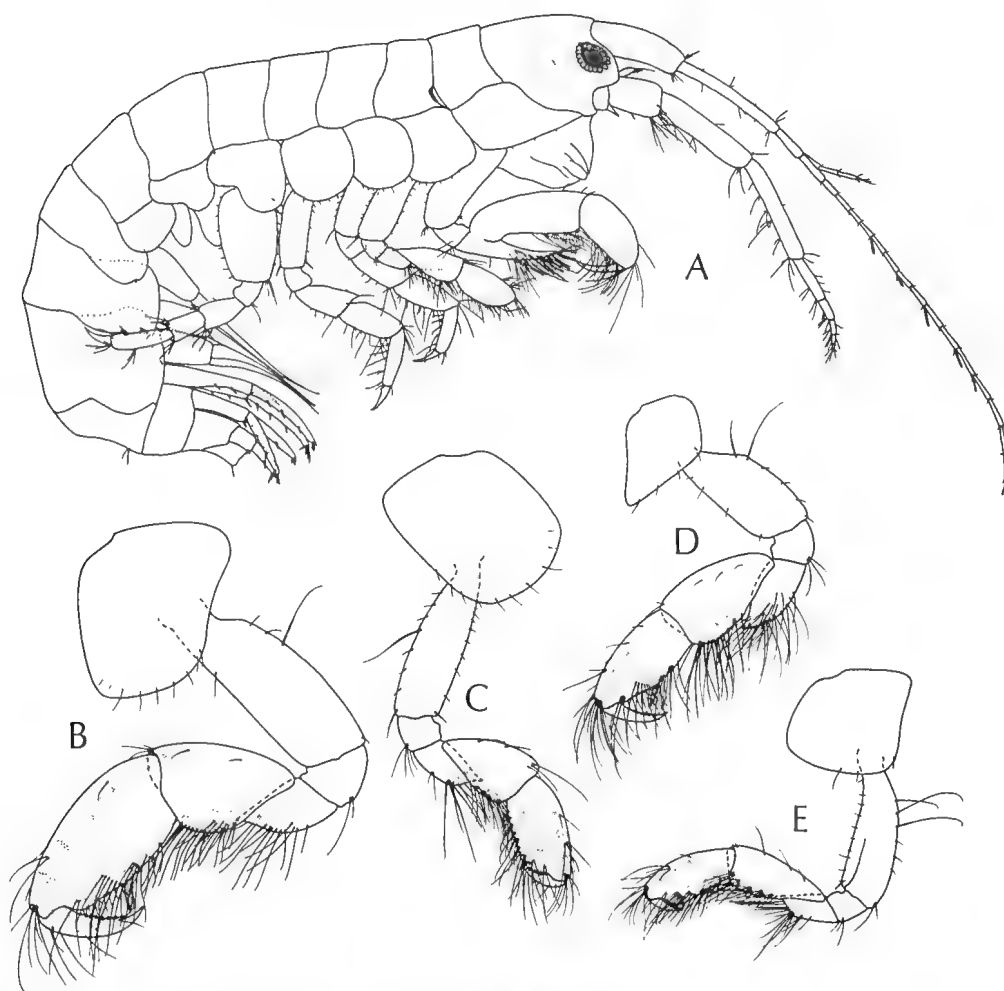


Fig. 11. *A. hircosa*, Tinderbox. A, ♂ lateral view; B, ovigerous ♀ gnathopod 1; C, ovigerous ♀ gnathopod 2; D, subadult ♂ gnathopod 1; E, hyperadult ♂ gnathopod 2.

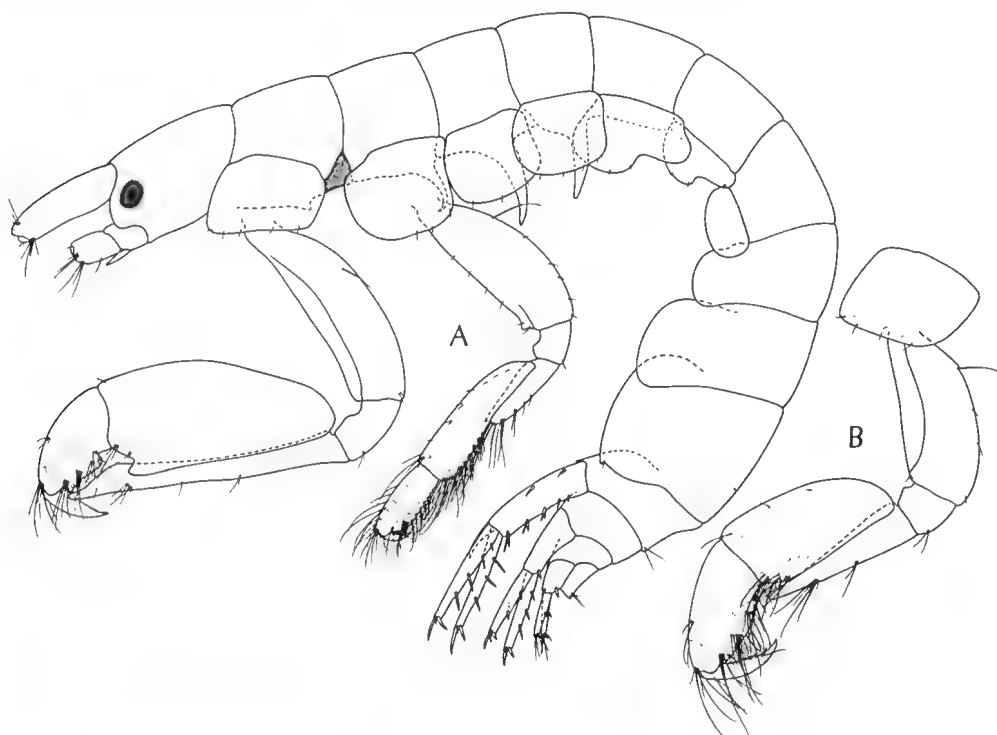


Fig. 12. ♂ *A. adpressa*, Western Port. A, lateral view; B, subadult gnathopod 1.

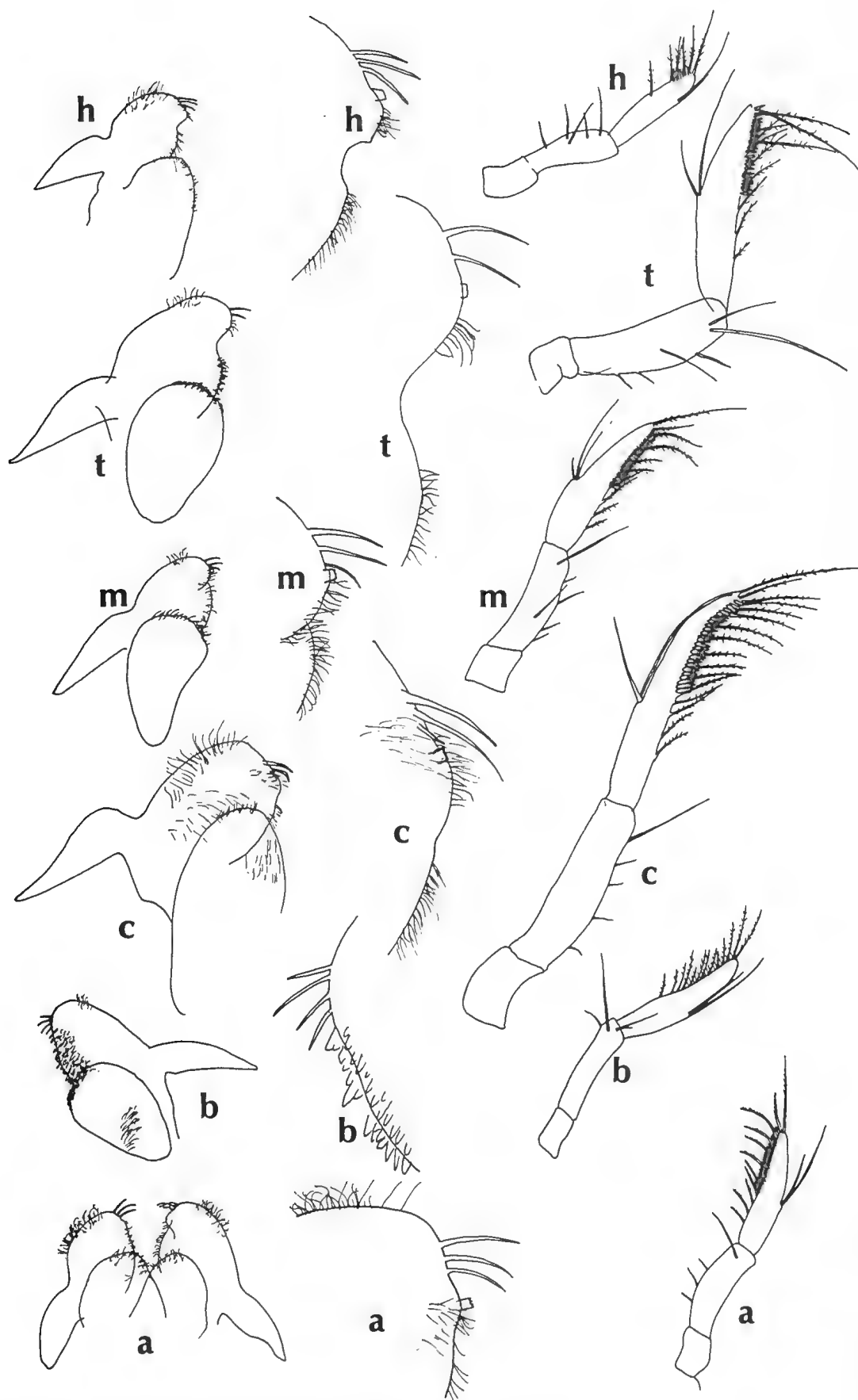


Fig. 13. Labium and mandibular palp of Australian and New Zealand *Aora* spp. h = *A. hircosa*, t = *A. typica*, m = *A. mortoni*, c = *A. maculata*, b = *A. hebes*, a = *A. adpressa*.

reaches the end of the carpus of the same appendage but does not do so in *A. atlantidea*.

World distribution. Tasmania to Victoria.

Aora adpressa n. sp.

Figs 2, 12, 13

Type material. HOLOTYPE: ♂ 6.00 mm. 2 km W of Phillip Island, Western Port, Victoria (Western Port Bay Environmental Study Station 1747), 1973-74. NMV J. 1322. PARATYPES 3♂. Same data as holotype. NMV J1323.

Etymology. The name refers to the fusion of the merus with the posterior margin of the carpus in the male gnathopod 1.

Diagnosis. Maximum length 6.0 mm. Male pereon segments 2-4 with strong sternal processes, on segment 2 slender, strongly curved forward, on segments 3-4 stouter, weakly curved forward. Male gnathopod 1 coxa subrectangular, anterodistal corner unproduced; basis and ischium moderately slender; merus slender, much longer than carpus, fused to posterior margin of carpus throughout the length of the carpus, the free end swollen basally, constricted distally, subacute; propodus less than half length of carpus, posterior margin produced into a broadly bilobed medial flange; dactylus stout, about two-thirds length of propodus, opposable to free end of merus. Male gnathopod 2 elongate only moderately setose, palm very oblique.

Female unknown.

Description. Head ocular lobes moderately produced, obtuse; eye subround. Male gnathopod 2 carpus very elongate and slender, propodus slender, scarcely more than half length of carpus, dactylus fitting palm. Pereopods 3-7 unknown. Epimera 1-2 rounded, epimeron 3 with small posterodistal tooth. Uropod 1 peduncle with strong, spiniform interramal process. Uropod 2 with rudimentary interramal process. Uropod 3 rami subequal, outer ramus with small second article. Colour in alcohol pale tan without distinct markings.

Discussion. *Aora adpressa* is unique among known *Aora* spp. in having the merus fused to the carpus throughout the latter's length. The opposition of the free end of the merus to the propodus results in a superficial similarity to species of *Microdeutopus*. Myers (1981) described a new genus of Aoridae (*Aorella* Myers) from Fiji, which possesses a male gnathopod 1 extraordinarily like that of *A. adpressa*. His observation that "in all known male *Aora* the merus is fused to the carpus only at the base, being free distally" is clearly no longer tenable. *Aorella* differs from *Aora* in the complexly subchelate male gnathopod 2, strongly produced distoventral cephalic margin, flanged article 3 of antenna 2 and reduced mandibular palp. The present species exhibits none of these characters. The very similar gnathopod 1 of *A. adpressa* and *Aorella*

multiplex may be due to convergence or *A. adpressa* may represent an early stage in the development of *Aorella* from *Aora*.

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High Pressure Minerals and the Origin of the Tertiary Breccia Pipe, Ballogie Gem Mine, near Proston, Queensland

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ABSTRACT. High pressure minerals found in Miocene basaltic volcanics at Ballogie include large garnets, aluminous clinopyroxenes and orthopyroxenes, olivine, kaersutitic amphibole, anorthoclase and opaque oxides; they occur together with minor amounts of biotite, corundum and zircon. The garnet, some pyroxenes and anorthoclase can be of gem quality. The minerals accompany abundant lherzolite xenoliths in the volcanics and resemble some other occurrences in SE Queensland.

A magnetic survey of the site suggests a diatreme composed largely of breccia intruded by small basaltic bodies. The garnet ($\text{Mg}_{62-66} \text{Fe}_{21-24} \text{Ca}_{12-14}$), clinopyroxenes ($\text{Mg}_{49-56} \text{Ca}_{34-39} \text{Fe}_{10-13}$, with 6.7–8.5% Al_2O_3) and orthopyroxenes ($\text{Mg}_{81-84} \text{Fe}_{12-15} \text{Ca}_{3-4}$, with 4.8–5.8% Al_2O_3) probably represent xenocrysts derived from garnet pyroxenites and pegmatitic garnetites interlayered with spinel lherzolite mantle. The compositions suggest that these minerals crystallized under pressure-temperature conditions around 14–15 kb and 1000–1100°C. The Ti content of the kaersutites, using a new geobarometer, gives approximate pressures of crystallization mostly between 12 kb and 14 kb.

The bulk of the Ballogie minerals were sampled from a volatile-bearing upper mantle, relatively rich in Ti, but poor in Cr. The model invoked for the emplacement of a composite diatreme such as the Ballogie pipe involves sudden outgassing above a rising diapir by crack propagation. The resultant updrag also provides the potential to transport very deep material from the diamond stability zone.

HOLLIS, J.D., F.L. SUTHERLAND & R.E. POGSON, 1983. High pressure minerals and the origin of the Tertiary breccia pipe, Ballogie Gem Mine, near Proston, Queensland. *Records of the Australian Museum* 35(4): 181–194.

In 1981 Mr E.A. Thomson of Boondooma, Queensland asked the Department of Mineralogy and Petrology at the Australian Museum to investigate his gemstone lease at Covert Creek, 17 km SSW of Proston (151°31.5' E, 26°18.0' S). The Ballogie Gem Mine, on the east side of the creek, yields gem-quality red garnet, comparable with the Garnet Gully prospect 10 km west at Brigooda (Queensland Geological Survey, 1981). The fragments come from a small alkali basalt exposure within granite country rock. (Fig. 1.) An anorthoclase megacryst from the basalt gave a K-Ar age of 16.0 ± 0.2 Myr, interpreted as the age of eruption (Sutherland & Wellman, in prep.). Other prominent minerals brought up by the basalt include olivine, pyroxenes and oxides, typical of high pressure megacryst suites found in eastern Australia (Wass & Irving, 1976). The Ballogie basalt is not mapped, but lies amongst the northern Main Range Volcanics of south-eastern

Queensland (Murphy *et al.*, 1976). It belongs to a younger episode than the bulk of these basalts and is not lateritized.

The site has potential for gem production and possible diamond exploration (Queensland Geological Survey, 1981) and was visited by the Museum in November 1981 and May 1982. Extensive collections were made of the volcanic inclusions by Hollis and Sutherland and a magnetometer survey was made over the basaltic body by Pogson. This paper deals with the form of the basalt and the mineral inclusions. A more detailed study of the Ballogie basalt will be given in a wider petrogenetic study involving the other basalt bodies and their inclusions from the Brigooda region, under study by the Australian Museum in association with A.D. Robertson, Geological Survey of Queensland. The geophysical survey carried out by the Museum in May 1982 was the first in the institution's history.

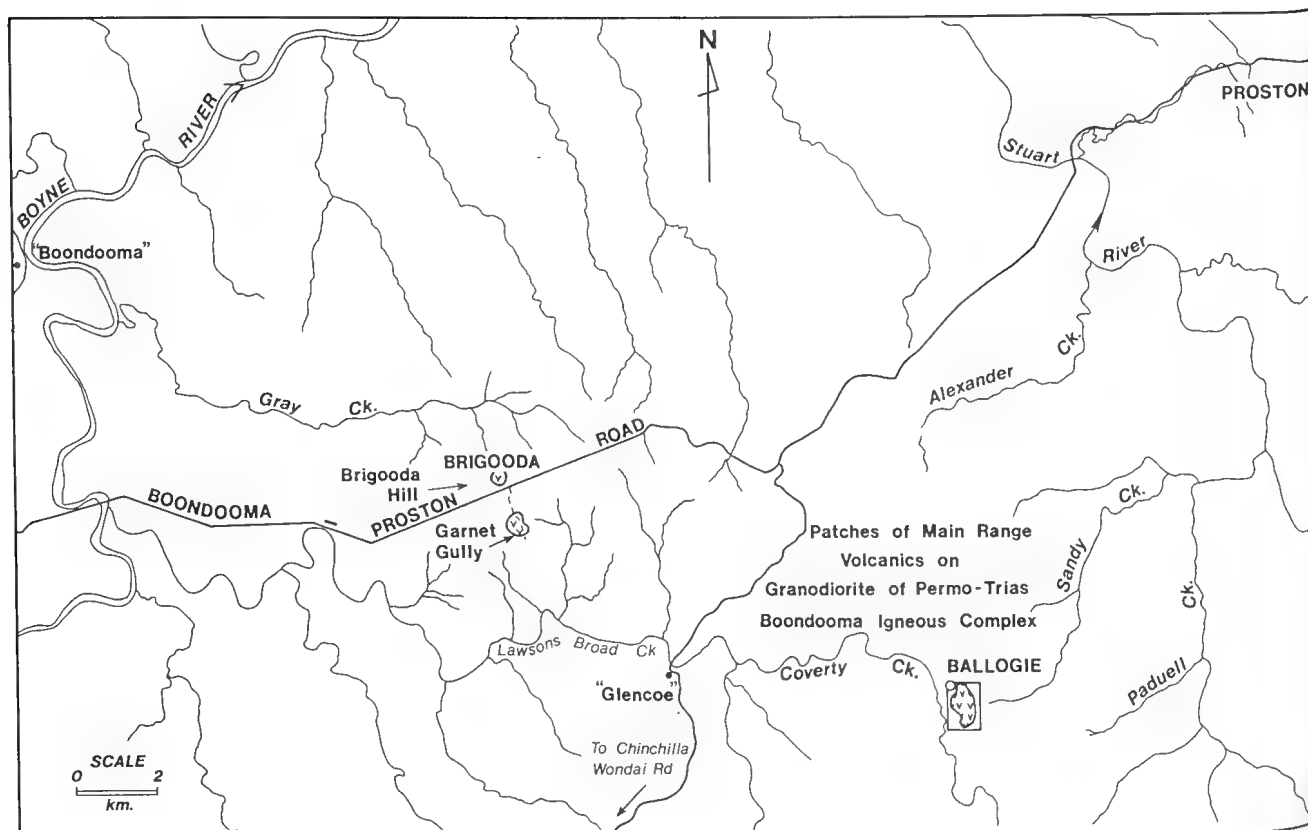


Fig. 1. Locations of Ballogie and Brigooda diatremes, Proston district, showing area of Ballogie magnetic survey.

Table 1. Comparative census of mineral inclusions in Ballogie and Brigooda volcanics.

*Basalt breccia, Ballogie; Test Hole No.1,
Coarse Fraction (5 mm & over).
Weight per cent.*

Total pyroxenes	78.4%
(a) Rough pyroxenes with alterations	46.8%
(b) Ablated black pyroxenes	31.6%
Pyrope-almandine	7.8%
Pleonaste - Cr pleonaste	5.9%
Amphibole	4.7%
Magnetite	1.4%
Ilmenite	1.1%
Anorthoclase	<1%
Zircon	<1%

*Massive basalt, Ballogie; NW side of hill.
Volume per cent.*

Lherzolite xenoliths	65.2%
Pyroxenes	20.8%
Anorthoclase	3.4%
Amphibole	<1%
Garnet-bearing inclusions	very rare

*Massive megacryst basalt,
Garnet Gully, Brigooda.
Volume per cent*

Amphibole	48.7%
Lherzolite	33.2%
Pyroxenes	11.0%
Garnet-bearing inclusions	3.6%
Anorthoclase	<1%

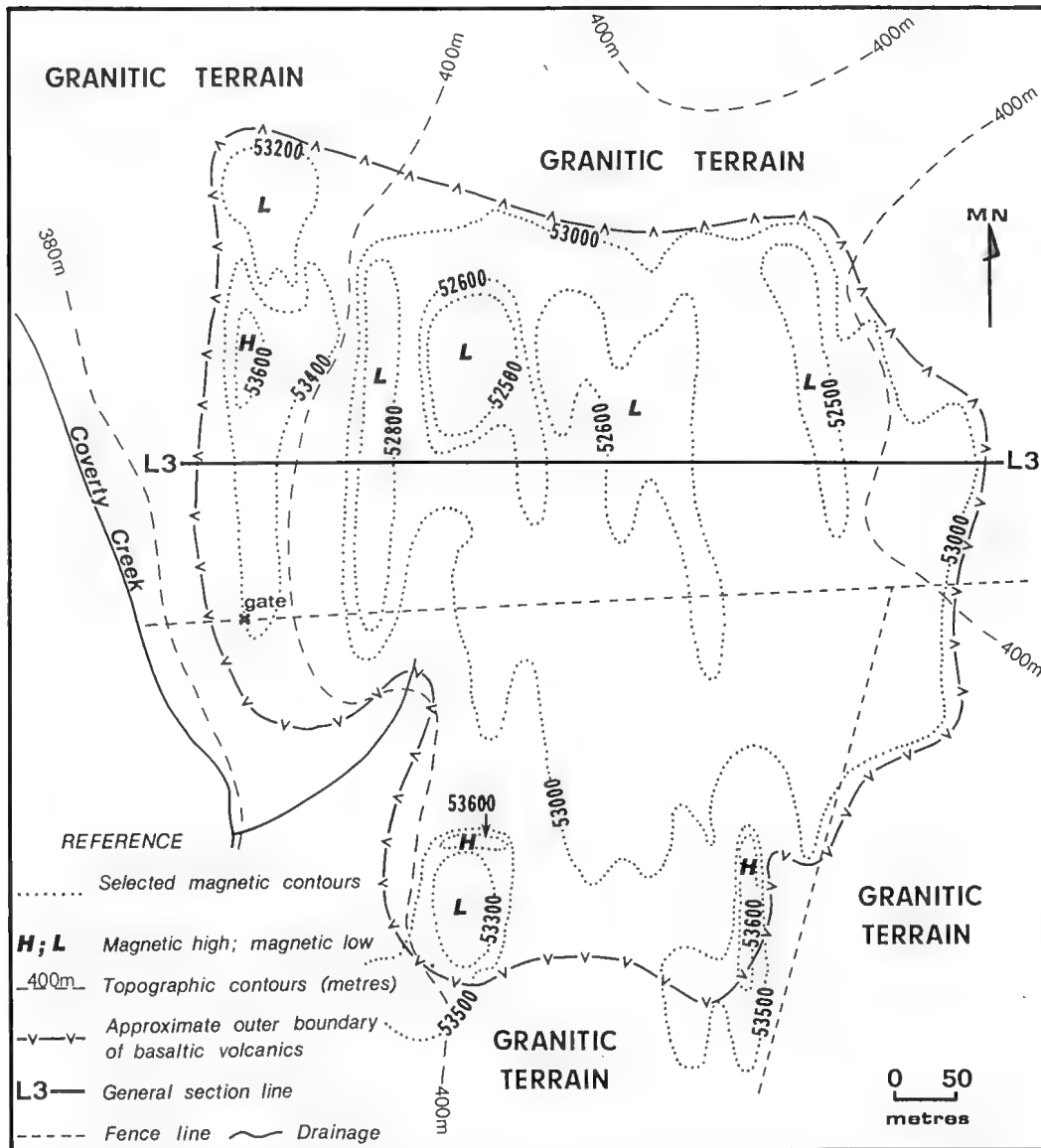


Fig. 2b. Summary diagram of magnetic survey in relation to general topography and inferred geology.

The Ballogie Occurrence

The basalt forms a flat-topped convex-sloped hill about 0.6 km long and 0.5 km wide, surrounded by float and granite showing NW-SE joint systems. The granites include porphyritic and graphic types with veins of tourmaline-bearing pegmatites and quartz. Gem-bearing gravels on the NW side of the hill contain both granite and basalt fragments. The relationships of the country granite to the basalt are not clearly exposed, but an anomalously high content of gem garnet is found in the NW flank. Trenching in this area exposed a volcanic breccia composed of country rock, basaltic and granitic fragments, commonly enclosed in autoliths and usually partly altered by late-stage fluids.

The basalt in the rubble is massive and contains predominant ilmenite xenoliths and pyroxene megacrysts, but garnet is exceptionally rare (Table 1). In thin section, the basalt is a fine-grained alkaline

variety containing microphenocrysts of olivine in a groundmass with andesine-oligoclase laths, clinopyroxene grains and granular opaque oxides, with late-stage alkali feldspars and carbonate. It is petrographically similar to the K-rich hawaiite-mugearite series fractionated from alkali basalt magmas within some of the Queensland provinces (Green *et al.*, 1974).

The Form of the Anomaly

The magnetometer survey of the site (grid reference 527899, Murgon 1:100,000 Topographic Sheet 9245, Queensland) covered the basaltic hill (500 × 600 m area, 15 m elevation and 400 m a.s.l.) and its immediate environs out to 800 × 800 metres. The spacing of the grid, the method of data collection and magnetic susceptibilities measured on the rocks are given in the Appendix. The data are presented in a contour plan

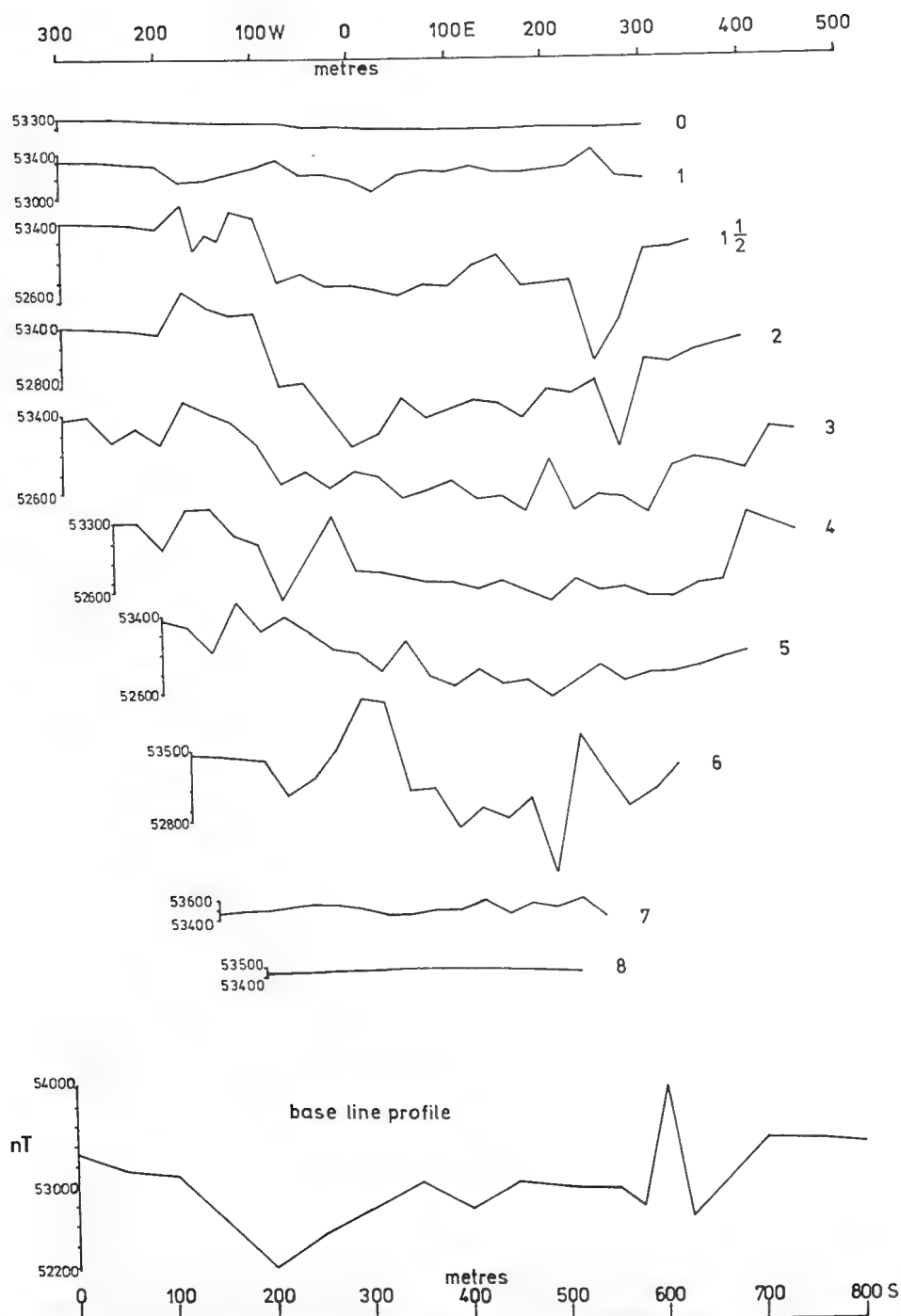


Fig. 3. Magnetic profiles based on section lines on magnetometer survey contour map.

(Fig. 2a), a summary plan (Fig. 2b) and profiles (Fig. 3). The magnetic trends and their interpretation are now discussed in some detail to reconstruct the form of the diatreme. Topographic effects due to magnetic material lying above some recording stations are considered negligible in this reconnaissance survey as the material has relatively low magnetic susceptibility.

The central feature of the contour plan is an ovoid anomaly system, about 500×600 metres orientated along a broad regional N to NNW trend. It is a magnetic low relative to background levels over the surrounding

granite. The profile shapes and intensities suggest a body of lower magnetic susceptibility than its surroundings with width much greater than depth to its top and extending to depth. Superimposed on the main anomaly are higher frequency components representing very localized narrow near-surface features, probably basaltic intrusives.

In view of the occurrence of breccia at the site, the geometry of the anomaly suggests a pipe-like diatreme, completely surrounded by granite and injected by minor basaltic intrusives towards its margins. The bulk of the

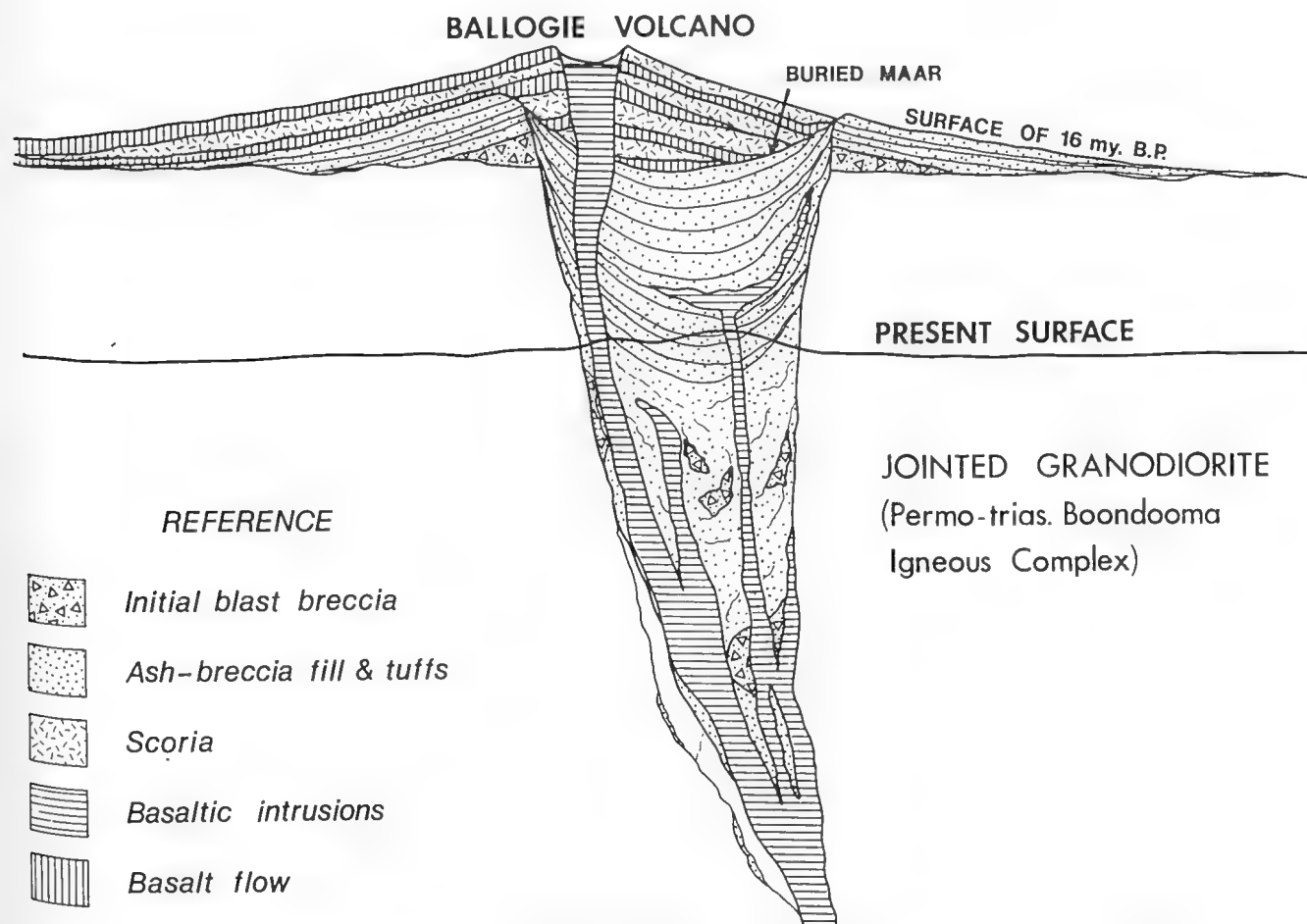


Fig. 4. Hypothetical reconstruction of the Ballogie volcano. Section shows present level of erosion exposing an ash-breccia-filled diatreme and associated basaltic intrusions.

inferred pipe is enclosed within the 53,000 nT contour line and the contour plan indicates internal complex inhomogeneities of unknown nature.

The core of the anomaly (450×550 m) is well-defined with high gradients at its edges (e.g. 75–100 m W, lines 1–4). It divides into smaller and more intense magnetic lows, especially towards its northern edge (e.g. 0 m and 75 m E, line 2, and 250 m W, line 1½). Their precise nature is unclear due to poor exposure, but complex brecciated or tuffaceous material on available evidence seems more likely than extensive alteration zones in massive basalt. The more intense lows (e.g. 0 m, between lines 6 and 7) may represent limited shallow inhomogeneities with little or no basaltic content.

A small poorly defined magnetic low (100×50 m) occupies flatter land adjoining the NW edge of the main anomaly. Nine test pits here revealed tuffaceous or brecciated volcanics at shallow depth (0.6–1.1 m). A vesicular, hornblende-rich basaltic breccia (pit No. 4) marks a spot high in the magnetic low. Pulverized granite breccia lies near the granite contact (pit No. 7, at 186 m W, line 1). The zone therefore contains material of variable composition, and could involve

complex intrusive relationships near the granite contact.

Narrow linear highs and separate small isolated highs occur along the W and S margins of the pipe over three main areas of rubbly basalt scree. The linears are traceable for up to 300–400 m as northerly trending zones a few tens of metres wide (N and S of 175 m W, line 2); more restricted anomalies occur at 0 m, line 6 and 175 m E, line 7 (40 m basalt spur). The sharpness and small wave-length of the magnetic signature patterns suggest localized shallow sources. A similar linear feature on the NE boundary of the pipe traceable over 150 m, however, is a magnetic low of unknown cause. The N-S elongations in the anomaly pattern may partly reflect effects from the rectangular grid pattern of the survey.

All profiles (Fig. 3) show similar broad features—almost flat curve segments over granite at the extremes and a trough of variable width (250 to 600 m) in the middle. The trough narrows N and S. Several smaller scale troughs and peaks can be correlated across traverse lines, defining northerly-trending linear features. Small irregular peaks may represent localized intrusives. The N-S base-line has a high peak at 600 m S (over basalt rubble) and a small trough at 200 m S (repeated on traverse lines 6 and 2). The base-line low lies on the

northern slopes of the hill, near a shallow saucer-like depression.

The relative magnetic susceptibilities of the rocks are basalt > granite > breccia and the magnetic readings over the structure (Appendix) are compatible with a breccia pipe, structurally emplaced along a fracture pattern in the intruded granites. This pipe gives a 1400–1500 nT negative anomaly below the granite background levels. A generalized reconstruction of the form of the various rock units that make up the pipe is given in Fig. 4. This is based on the section line in the summary map of the magnetic and geologic data shown in Fig. 2b.

The Mineral Suite

The Ballogie volcanics contain many large grains of red garnet, bright green to brown and black clinopyroxenes, dull green to black orthopyroxene, dark kaersutite, white to clear feldspar and opaque oxides including spinel, ilmenite, titano-magnetite and magnetite. Olivine (Mg_{90}) is common, disaggregated from abundant lherzolite xenoliths, but is generally decomposed to greenish chlorite and serpentine. The garnet, both types of pyroxenes and anorthoclase include gem quality material, but not the olivine. A census of mineral species in typical breccia and the main minerals found in the massive basalt at Ballogie are compared in Table 1.

Table 2. Garnet xenocryst analyses, Ballogie and SE Queensland occurrences.

Locality:	Bal.158	Bal.161	Bal.191	Bal.194	Brig.I.J.	Nan.G21	Low.5/1	WOW 3/1
SiO ₂	40.86	41.22	41.03	41.93	40.48	41.46	41.38	40.79
TiO ₂	0.50	0.42	0.46	0.42	0.47	0.24	0.41	0.66
Al ₂ O ₃	23.59	23.38	23.55	22.86	22.98	22.57	23.36	22.62
Cr ₂ O ₃	0.00	0.00	0.00	0.00	0.00	0.30	0.05	0.02
Fe ₂ O ₃					1.56			
FeO (see note)	12.55	11.79	10.65	11.26	12.07	10.32	10.55	14.19
MnO	0.36	0.33	0.34	0.34	0.43	0.24	0.32	0.36
MgO	17.87	18.24	18.79	17.91	16.54	18.10	18.56	15.88
CaO	5.34	5.29	5.19	4.91	5.35	5.16	5.19	5.54
Na ₂ O	0.05	0.05	0.03	—	—	0.05	—	—
TOTAL	100.12	100.72	100.04	99.64	99.88	98.44	99.82	100.06
Cation								
Si	5.8586	5.9079	5.8897	6.0415	5.892	6.0675	5.9458	5.9571
Ti	0.0535	0.0457	0.0496	0.0456	0.052	0.0263	0.0443	0.0721
Al	3.9862	3.9490	3.9837	3.8812	3.942	3.8700	3.9557	3.8929
Cr	—	—	—	—	—	0.0345	0.0059	0.0019
Fe ³⁺					0.110			
Fe ²⁺ (see note)	1.5051	1.4126	1.2791	1.3574	1.470	1.2548	1.2675	1.7326
Mn	0.0436	0.0404	0.0418	0.0420	0.052	0.0293	0.0389	0.0447
Mg	3.8195	3.8974	4.0219	3.8464	3.588	3.9240	3.9716	3.4556
Ca	0.8202	0.8117	0.7977	0.7977	0.834	0.8040	0.7995	0.8666
Na	0.0150	0.0136	0.0096	—	—	0.0143	—	—
TOTAL	16.0997	16.0783	16.0731	16.0118	15.940	16.0247	16.0281	16.0235
Cation ratios:								
Mg	62	64	66	64	60	65	53	45
Fe	25	23	21	23	25	21	32	40
Ca	13	13	13	13	14	13	15	15

Bal.: Ballogie; Brig: Brigooda; Nan: Stony Pinch, Nanango; Low: Lowood; WOW: Pheasants Creek, Wowan. Ballogie & Nanango analyses, J.D. Hollis; Brigooda analyses, I. Jackson, Research School of Earth Sciences, Australian National University; Lowood and Wowan analyses, L. Rayner, Geology Dept, Sydney University. Electron microprobe analyses, with Fe as total FeO except for the Brigooda analysis. Cation contents are based on 24 oxygens. Cation ratios show the relative ionic proportions of three selected components.

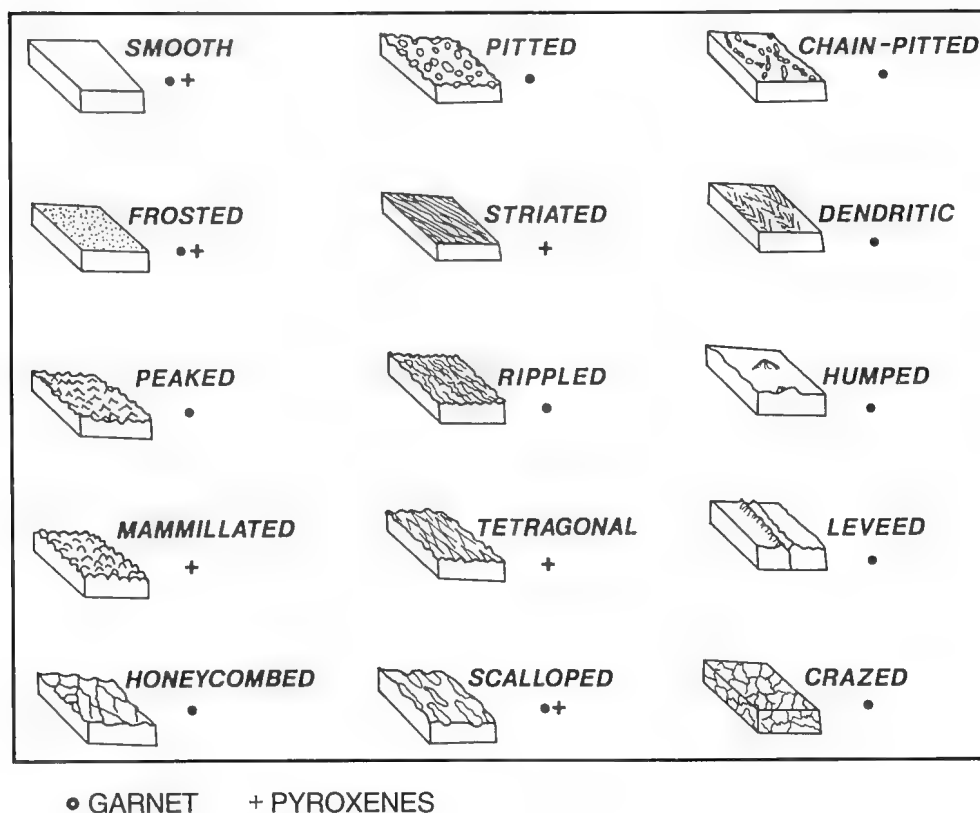


Fig. 5. Types of surface features observed on mineral grains in the Ballogie and Brigooda diatremes. For scale, the front width of units represents 3 mm and the side length 5 mm.

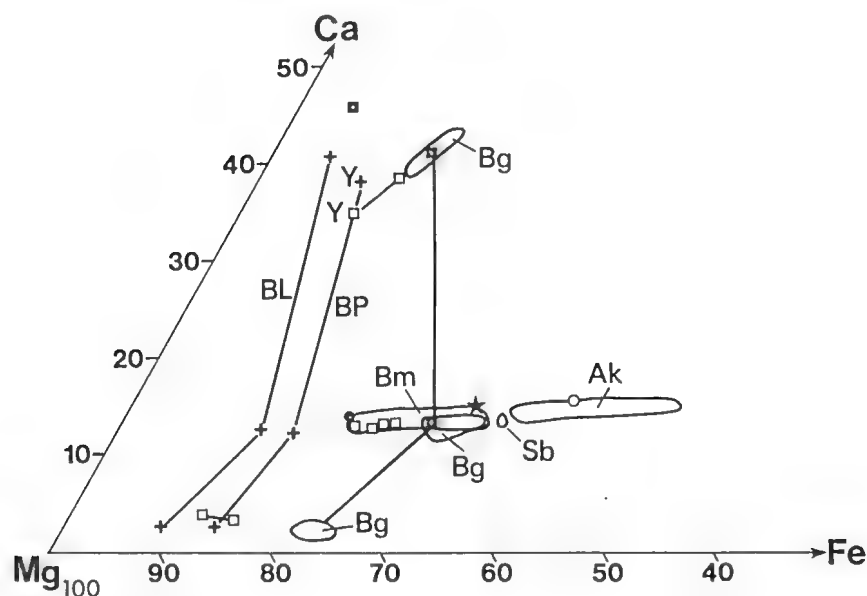


Fig. 6. Comparative Ca-Mg-Fe plots of pyroxene and garnet xenocrysts from Queensland occurrences (points) in relation to fields of these minerals from selected E. Australian xenolith sites (closed areas). Xenocryst plots are shown from Ballogie (open squares) Brigooda (closed squares), Nanango (closed circle), Lowood (asterisk), Wowan (open circle) and Yatton Creek (Y). Xenolith fields are shown for Bow Hill garnet lherzolite (BL) and garnet pyroxenite (BP), Tasmania; Brigooda garnet pyroxenites (Bg) and S. Mt. Barngogo, Monto, garnet pyroxenite (Sb), Queensland; Bullenmerri garnet pyroxenites (Bm) and Anakie E. Hill felsic to mafic granulites (Ak), Victoria.

Distinctively sculptured surfaces are found on many of the mineral grains, similar to those described from kimberlites of Yakutia, Siberia (Frantsesson, 1970). Textures observed at Ballogie and on grains from the similar Brigooda pipes are given in Fig. 5. These surface features may be caused by corrosion in a gaseous medium, abrasion due to collisions with particles and etching occasioned by alteration planes through crystals. They provide a record of the origin and transportation history of the grains.

The gem garnets for which Ballogie is noteworthy reach up to 4 cm across and come from the pyroclastics. They are pyrope almandines ($n = 1.754$; all refractive indices were measured in the D-line of Na and corrected to 20°C, with error ± 0.003) and have relatively high Ti and low Ca and Cr contents, showing a limited compositional range (Table 2, Fig. 6). They are magnesian, but close to garnets from the adjacent Brigooda occurrence, and in some garnet pyroxenites in eastern Australian alkali basalts (Sutherland & Hollis,

Table 3. Pyroxene xenocryst analyses, Ballogie and Queensland occurrences.

Locality:	Bal.192	Bal.193	Bal.198	Bal.199	Brig.I.J.	Brig.A8	Yat.C2	Yat.C2a
SiO ₂	51.66	54.36	54.09	50.71	49.84	52.03	50.98	51.97
TiO ₂	0.45	0.14	0.28	0.85	0.94	0.50	0.44	0.24
Al ₂ O ₃	6.70	4.78	5.76	8.54	9.23	6.55	9.04	7.47
Cr ₂ O ₃	0.37	0.52	0.00	0.00	0.00	0.91	0.02	0.02
Fe ₂ O ₃					1.50			
FeO	5.86	7.57	9.35	6.87	5.60	2.96	5.28	4.81
MnO	0.14	0.12	0.16	0.15	—	0.05	—	—
MgO	17.75	29.59	28.23	15.24	14.88	14.96	16.86	18.23
CaO	15.38	1.97	1.73	16.45	16.61	19.84	16.67	16.12
Na ₂ O	1.21	0.23	0.20	1.43	1.52	1.68	0.73	0.47
TOTAL	99.57	99.30	99.79	100.26	100.11	99.48	99.99	100.91
Cation								
Si	1.8740	1.9086	1.8995	1.8393	1.810	1.868	1.8347	1.8643
Ti	0.0122	0.0038	0.0074	0.0233	0.026	0.014	0.0120	0.0066
Al	0.2865	0.1979	0.2383	0.3652	0.395	0.277	0.3833	0.3158
Cr	0.0105	0.0144	—	—	—	0.026	—	0.0196
Fe ³⁺					0.041			
Fe ²⁺	0.1777	0.2223	0.2747	0.2084	0.170	0.089	0.1589	0.1443
Mn	0.0043	0.0037	0.0048	0.0047	—	0.001	—	—
Mg	0.9597	1.5489	1.4778	0.8242	0.805	0.801	0.9043	0.9749
Ca	0.5979	0.0742	0.0650	0.6393	0.646	0.763	0.6429	0.6195
Na	0.0854	0.0155	0.0134	0.1009	0.107	0.117	0.0511	0.0326
TOTAL	4.0082	3.9893	3.9809	4.0053	4.000	3.956	3.9872	3.9776
Cation ratios:								
Mg	55	84	81	49	48	48	53	56
Fe	10	12	15	13	13	6	9	8
Ca	35	4	4	38	39	46	38	36

Temperature determinations from pyroxene pairs:

	Cpx 192 + Opx 193	Cpx 199 + Opx 198
Wood & Banno temp. (°C)	1248	1152
Wells temp.	1236	1141

Bal.: Ballogie (192 and 199 Cpx, 193 and 198 Opx); Brig.: Brigooda (Cpx); Yat.: Yatton Creek (Cpx). Ballogie analyses, J.D. Hollis; Brigooda analyses, I. Jackson, Research School of Earth Science, Australian National University; Yatton Creek, unpublished analyses, F.L. Sutherland (Sutherland, 1980). T for pyroxene pairs Bal. 192-193 and Bal. 198-199 from Wood and Banno (1973) and Wells (1977) methods. Electron microprobe analyses, with Fe as total FeO except for Brigooda analysis. Gemmy pyroxenes are Bal. 192 (green Cpx) and Bal. 199 (amber brown Opx). Analysis A8 is a Cr-bearing diopside xenocryst from lherzolite for comparison. Cation contents are based on 6 oxygens.

1982). However, the sizes of the masses found at Ballogie and Brigooda are associated with garnetites. They contain interlocking anhedral up to 10 cm diameter with vague banding and provide cuttable gems to over a hundred carats weight.

The pyroxenes reach over 10 cm across, and are the commonest species in the heavy mineral concentrates. Most are dull greyish to shiny black augites and bronzites (Table 3), but over a bright light they separate into semi-transparent green Cr-bearing endiopsidic augite (α 1.682, β 1.687, γ 1.706) and amber brown bronzite (α 1.677, β 1.680, γ 1.685).

The amphiboles are almost as common as pyroxenes and show TiO_2 contents typical of kaersutites (α 1.677 pale yellow-brown, β ~1.685 brown to red-brown, γ 1.708 dark yellow-brown). Kaersutite megacrysts from Queensland occurrences vary considerably in composition, but those from Ballogie are relatively rich in alkalis and define a limited homogeneous field (Table 4). This field falls across typical kaersutite compositions

for megacrysts elsewhere in eastern Australia (Sutherland & Hollis, 1982) for Mg-Fe-Ti.

Feldspars of the K-oligoclase/anorthoclase series are common associates of the fractionated Queensland basalt lineages (Table 5). The Ballogie feldspar is sodic anorthoclase (α 1.529, β 1.532, γ 1.534).

Opaque oxides at Ballogie include black spinel as a low Cr-pleonaste which may be euhedral, Mg-bearing ilmenite and members of the magnetite-ulvospinel series (Table 6). Other rare minerals in the suite are biotite, zircon and corundum.

Origin of the Minerals

The lherzolite xenoliths in the Ballogie basalt indicate transport in fractionated magma eruptions from the mantle. Clinopyroxene xenocrysts are similar in compositional range to the brown to greenish xenocrysts derived from spinel clinopyroxenite in a basalt plug at Yatton Creek, North Queensland (Sutherland, 1980).

Table 4. Amphibole megacryst analyses, Ballogie and Queensland occurrences.

Locality:	Bal.1A	Bal.3A	Bal.5	Brig. 1	SB 2R	Nebo 2	Nebo 3	Mt. Mit.
SiO_2	39.87	40.01	40.14	39.93	39.58	41.63	39.82	39.8
TiO_2	5.06	4.96	4.90	5.52	5.06	5.47	5.74	4.6
Al_2O_3	14.42	13.81	14.02	14.31	13.97	16.36	15.14	14.2
FeO^r	11.96	15.61	15.16	11.62	11.99	10.36	12.61	13.0
MnO	0.10	0.15	0.23	0.01	0.12	<0.02	<0.02	<0.2
MgO	12.06	9.60	9.60	11.62	11.51	9.55	11.43	11.9
CaO	10.22	9.79	9.60	9.79	10.03	10.39	10.42	9.8
Na_2O	2.90	2.93	3.00	3.17	2.93	4.71	2.72	2.8
K_2O	2.08	2.05	2.07	2.07	1.83	1.42	1.99	1.3
TOTAL	98.69	98.91	98.66	98.04	97.02	99.89	99.87	97.4
Cation								
Si	5.695	5.820	5.802	5.642	5.9300	5.9869	5.8075	
Ti	0.544	0.542	0.534	0.587	0.5701	0.5923	0.6296	
Al	2.428	2.368	2.389	2.383	2.4676	2.7727	2.6027	
Fe^{2+}	1.429	1.899	1.833	1.378	1.5024	1.2458	1.5375	
Mn	0.012	0.018	0.029	0.001	0.0152	—	—	
Mg	2.569	2.082	2.069	2.448	2.5700	2.0478	2.4855	
Ca	1.564	1.527	1.486	1.483	1.6102	1.6016	1.6280	
Na	0.802	0.828	0.840	0.868	0.8512	1.3145	0.7696	
K	0.380	0.380	0.380	0.373	0.3498	0.2603	0.3711	
TOTAL	15.423	15.464	15.353	15.163	15.8665	15.8219	15.8315	
Cation ratios:								
Mg	57	46	47	56	55	53	53	
Fe	31	42	41	31	34	32	33	
Ti	12	12	12	13	11	15	14	

Bal.: Ballogie; Brig:Brigooda; SB: South Mt. Barngogo; Nebo 2: Weetalaba; Nebo 3: Redcliffe Tableland; Mt. Mit.: Mt. Mitchell. Ballogie & Brigooda analyses, F.L. Sutherland; Nebo analyses unpublished from Sutherland (1980); South Mt. Barngogo analysis, L.M. Barron; Mt. Mitchell analysis from Green *et al.*, (1974). Electron microprobe analyses, with Fe as total FeO. Cation contents are based on 23 oxygens.

The Yatton Creek basalt only contains spinel lherzolite xenoliths, suggesting a mantle association for such clinopyroxenes. The Ballogie orthopyroxenes (Mg_{84-88}) typify those commonly found within mantle-derived xenoliths in eastern Australia (Mg_{78-90} ; Bullenmerri; Griffin *et al.*, 1983) and are more Mg-rich than those typical of crustal granulites (Mg_{54-76} ; Nebo, Anakie E. and Tasmania; Sutherland, 1980; Sutherland & Hollis, 1982; Wass & Hollis, 1983). If it is assumed that the pyroxene pairs crystallized together, then temperatures of equilibration fall within the range 1140°C–1250°C (Table 3).

The garnets at Ballogie have restricted Ca/Mg + Ca + total Fe and fall within an almost straight line relationship with other garnet xenocryst plots from other basaltic occurrences in eastern Australia (Fig. 6). This relatively constant Ca compositional range tends to show increasingly higher pressure associations with increasing Mg relative to Fe (Hollis and Sutherland, 1983). The Ballogie garnets lie between the fields of high Mg garnet xenoliths (c. 22–24 kb origin, Bow Hill, Tasmania; Sutherland *et al.*, 1983) and transitional crustal garnet granulite fields (12–18 kb, Anakie E.; Wass & Hollis, 1983), and close to garnet compositions in mantle pyroxenites from Bullenmerri (1000–1110°C, 14–15 kb; Griffin *et al.*, 1983).

Further pressure constraints for the Ballogie suite are

provided by the kaersutites. Recent experimental work (Oba *et al.*, 1982) suggests that the Ti content in this mineral reflects the approximate pressure of crystallization (P) according to the equation $Ti = -0.013 (\pm 0.005) P + 0.69 (\pm 0.07)$. The exact constants of this are dependent on the general composition of the kaersutites. The Ballogie compositions are closest to those studied from Kakanui, New Zealand, for which Ti is $-0.006 P + 0.63$ (K. Yagi, pers. comm.). This is the first application of this geobarometer to Australian kaersutites, which at Ballogie gave a P range within 10–17 kb and mostly between 12–14 kb.

The pressure data indicate that most of the Ballogie suite crystallized at mantle depths. The anorthoclase, euhedral zircon and corundum, however, are more likely to be of crustal derivation (Stephenson, 1976; Hollis, 1982; Hollis & Sutherland, 1982), although anorthoclase can crystallize experimentally at pressures up to 15 kb in the presence of CO₂ (Arculus *et al.*, 1977).

The role of CO₂ in the crystallization of some of the minerals expelled in the Ballogie diatreme is indicated by abundant fluid inclusions with CO₂ in the pyroxenes and amphiboles. These are closely comparable to fluid inclusions found in mantle xenoliths at Wallabadah Rocks, New South Wales (Wass & Pooley, 1982) Anakie E. and Bullenmerri, Victoria (Wass and Hollis, 1983;

Table 5. Feldspar megacryst analyses, Ballogie and Queensland fractionated basalts.

Locality:	Bal.172	Nebo 1	Nebo 3	Nebo 4	Nebo 5	Nebo 7	AP 67	Mt. Mit.
SiO ₂	67.03	65.77	64.74	64.77	69.11	64.68	64.38	65.3
Al ₂ O ₃	20.47	20.85	21.87	21.91	16.58	22.05	22.03	21.7
FeO ^T	0.10	< 0.02	< 0.02	< 0.02	< 0.02	< 0.02	< 0.02	< 0.1
CaO	0.76	1.26	2.33	2.23	3.34	2.45	1.89	1.8
Na ₂ O	9.32	8.11	8.87	8.63	8.92	8.90	8.28	7.5
K ₂ O	2.56	4.01	2.01	2.46	2.05	1.92	2.87	2.3
TOTAL	100.23	100.36	99.42	99.75	99.56	99.85	100.05	98.7
Cation								
Si	11.7979	11.6425	11.4435	11.4433	12.1771	11.4113	11.450	
Al	4.2452	4.3505	4.5420	4.5618	3.4419	4.5821	4.619	
Fe ²⁺	0.0143	—	—	—	—	—	—	
Ca	0.1434	0.2398	0.4405	0.4214	0.6313	0.4632	0.360	
Na	3.1822	2.7846	3.0308	2.9551	3.0497	3.0451	2.855	
K	0.5741	0.9045	0.4531	0.5528	0.4604	0.4318	0.615	
TOTAL	19.9571	19.9219	19.9099	19.9344	19.7604	19.9335	19.899	
Cation ratios:								
Ca	4	6	11	11	15	12	9	10
Na	82	71	77	75	74	77	75	75
K	15	23	12	14	11	11	16	15

Bal.: Ballogie basalt, breccia; Nebo 1: Mt. St. Martin K-rich nepheline hawaiite; Nebo 3: Mt. Leslie K-rich nepheline mugearite; Nebo 4: Weetalaba K-rich mugearitic hawaiite; Nebo 5: Redcliffe Vale K-rich hawaiite; Nebo 7: Redcliffe Vale K-rich mugearitic hawaiite; AP 67: Arthur Peak hawaiite (Stephenson & Griffin, 1976). Mt. Mitchell nepheline benmoreite from Green *et al.* (1974). Ballogie analysis, J.D. Hollis; Nebo analyses, F.L. Sutherland, unpublished in Sutherland (1980). Cation contents are based on 32 oxygens.

Griffin *et al.*, 1983). These inclusions and the presence of amphibole and mica indicate significant amounts of volatiles were present in the mantle below these diatremes.

The available evidence suggests that most of the Ballogie xenocrysts come from a volatile-bearing mantle dominated by spinel lherzolite containing unusual layered pyroxenite-garnetite pegmatite intrusions. The minerals define an atypical Ti-rich, Cr-poor region of the eastern Australian mantle.

Discussion

The Ballogie volcano was one of several maar-producing outbursts north-west of Proston. These centres are of considerable interest as they document upper mantle petrology and include possible diamond sources, e.g. Brigooda (Geol. Surv. Qld, 1981). The apparent association between diamonds and alkali basaltic centres in eastern Australia has still to be proven, although growing evidence supports this association (Hollis & Sutherland, 1983). Experimental

temperature-pressure determinations when applied to Ballogie-Brigooda inclusions indicate upper mantle origins shallower than 60–70 km. For diamonds to be present in pyroclastics there would have to be at least a small component of much higher pressure (> 35 kb) mantle sampled. Other high pressure phases from this regime may be present, but equally rare and less distinctive to identify.

Geomagnetic data for Ballogie indicate a typical diatreme structure, the pyroclastics having been intruded by basalts at a later stage (Fig. 4.). Similar structures are widespread in eastern Australia; documented examples including Ruby Hill, Bingara (Lovering, 1964), Minchinbury, near Sydney (Crawford *et al.*, 1980) and some of the western Victorian maars (Ollier & Joyce, 1964). Isolated diamonds are found in all these provinces (e.g. McNevin, 1977).

High-pressure mantle minerals from many diatremes frequently contain inclusions and cavities rich in CO₂. Although many maars have involved groundwater from aquifer strata and surface drainage (Lorenz, 1973), the Ballogie eruptions were propagated via joints in a

Table 6. Opaque oxide xenocrysts, Ballogie and SE Queensland occurrences.

Locality:	Bal.196	Bal.197	Bal.150	Bal.149	Bal.195	Nan.II	Mt. Mit.	Mt. Mit.
SiO ₂	0.00	0.00	0.00	0.00	0.00	0.02	0.0	0.0
TiO ₂	0.94	1.19	35.11	51.23	46.77	49.98	51.5	25.4
Al ₂ O ₃	58.60	1.05	1.51	0.21	0.50	0.84	0.3	1.6
FeO ^T	25.08	91.45	56.24	44.96	50.39	42.69	42.7	67.0
MnO	0.10	0.31	0.35	0.45	0.34	0.14	0.9	0.9
MgO	15.43	0.29	2.86	3.71	2.04	4.24	3.8	2.5
NiO	0.07	0.00	0.00	0.00	0.00	0.08	0.0	0.0
CaO	0.00	0.00	0.00	0.00	0.00	0.02	0.0	0.0
TOTAL	100.22	94.29	96.08	100.57	100.04	98.01	99.2	97.4
Cation								
Si	—	—	—	—	—	0.0009		
Ti	0.0189	0.0295	0.9864	1.9112	1.8083	1.8313		
Al	1.8524	0.0407	0.0666	0.0125	0.0302	0.0489		
Fe ²⁺	0.5626	3.5229	1.7568	1.8653	2.1666	1.7569		
Mg	0.6167	0.0142	0.1595	0.2745	0.1566	0.3111		
Ni	0.0016	—	—	—	—	—		
Ca	—	—	—	—	—	—		
Mn	0.0016	0.0087	0.0110	0.0191	0.0149	0.0006		
TOTAL	3.0549	3.6160	2.9803	4.0826	4.1766	3.9497		
Cation ratios:								
Mg	51	1	5	7	4	8		
Fe	47	98	61	46	52	45		
Ti	2	1	34	47	44	47		

Bal.: Ballogie; Nan.: Stony Pinch, Nanango; Mt. Mit.: Mt. Mitchell. Bal. 196 pleonaste spinel, Bal. 197 magnetite, Bal. 150 ulvospinel, Bal. 149 ilmenite lamellae in ulvospinel, Bal. 195 ilmenite, Nan. II ilmenite, Mt. Mit. ilmenite core with titano-magnetite rim. Ballogie and Nanango analyses, J.D. Hollis; Mt. Mitchell analyses from Green *et al.*, (1974). Electron microprobe analyses, with Fe as total FeO. Cation contents for magnetite-ulvospinel are based on 4 oxygens and for ilmenite on 6 oxygens.

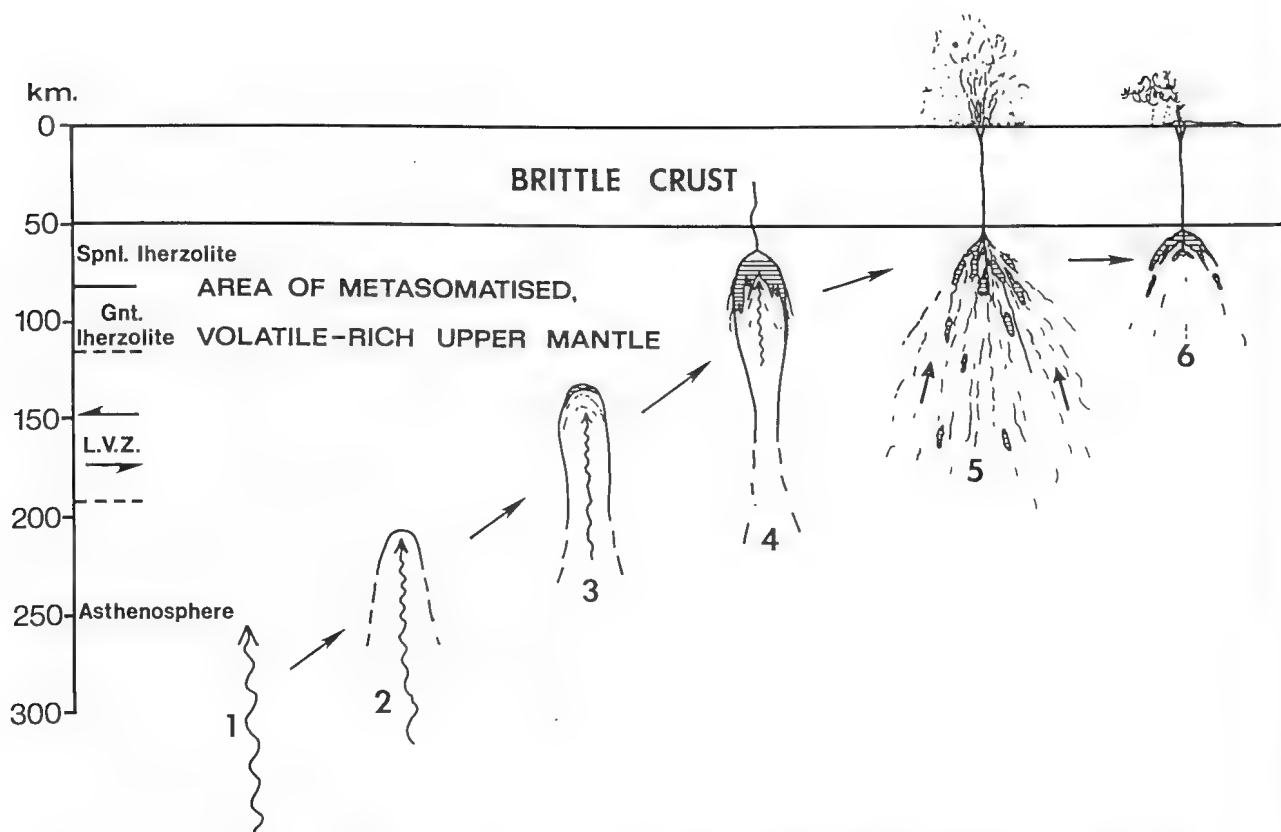


Fig. 7. Model depicting emplacement of magmas as composite diatremes, showing propagation of mantle heat anomaly and subsequent volcanism: Stage 1—deep asthenospheric 'hot spot' rises to produce 'thermal' above hot plume—Stage 2. Stage 3 shows 'thermal' rising to form diapir with associated low-degree of partial melting of mantle rocks. Magma and volatiles begin to accumulate (hatched zone). Stage 4 sees volatiles forcing crack to the surface via brittle or deep-faulted crust. Stage 5 involves immediate sudden and extensive outgassing; this rapidly brings up small amounts of deeper mantle material from 150 km to the surface. Maar develops at the surface with gentle, ash-producing eruptions, followed by nested cone formation and basaltic eruptions—Stage 6. The diatreme is partly intruded by alkaline magmas generated with larger-scale partial melting in the mantle above 80 km.

relatively elevated granitic topography. Mantle CO_2 is thus indicated as the major source of volatiles producing the Ballogie maar and possibly others in the district. The abundant amphiboles in the Ballogie breccia also suggest a volatile-rich and hydrous mantle beneath this part of Queensland. The amphibole content would vary and become minimal in the later basaltic eruptions as volatiles were expended (Table 1). Similar volatile-enriched mantle also occurs in other parts of eastern Australia (Sutherland, 1981; Wass & Hollis, 1983).

The distributions of high-pressure inclusions in diatremes like Ballogie show marked heterogeneity, with initial eruptive products containing the highest proportion of deep-seated inclusions (e.g. Bullenmerri; Hollis, 1981). These materials tend to be deposited as an initial agglomerate ring around the maar that is soon removed by erosion. If, as appears likely, diamonds are concentrated with initial blast materials, they will be comparatively rarer in subsequent ejecta and alluvial concentrates will contain grades higher than the deeper existing levels of the eroded pipes. Relics of initial blast material in diatremes tend to be concentrated around

the country rock contacts. Some of the highest diamond grades are found in these situations in the Kimberley Pipes of NW Australia (Kimberlites and Carbonatites, 6th Australian Geological Convention Symposium, Canberra, 1983). A similar pattern is anticipated for diatremes in eastern Australia.

In conclusion, the Ballogie occurrence suggests a model to explain propagation and emplacement of silica undersaturated magmas as composite diatremes (Fig. 7). Though CO_2 is the main volatile involved in this process at Ballogie, no carbonate replacement was noted in any alteration zones. Even if confined to fluid inclusions, the volume of CO_2 may have been substantial if gathered from a large region of metasomatized mantle. In the proposed model, crack propagation (Anderson, 1979) provides for sudden 'outgassing' at the head of a rising diapir. The depressurization may extend to depths well below the main zone of partial melting and xenolith entrainment, which is situated above 80 km. A fluidized system may entrain and rapidly transport (updrag) rare fragments of very deep material from the diamond stability zone, including diamonds. Such material should be sought at Ballogie.

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Appendix: Magnetometer Survey Details

The survey grid comprised an 800 m N-S (magnetic) base line, and nine E-W (325-750 m long) traverse lines at 100 m intervals numbered 0 to 8. A traverse line was added between lines 1 and 2 to show more detail in a particularly interesting region.

Data Collection

Readings were taken with a Scintrex MP-2 Proton Precession Magnetometer which measures total magnetic field to resolution ± 1 nT. For latitude 26°S , the earth's undisturbed total field magnitude is about 52,500 nT and the geomagnetic inclination is about 55°S (Breiner, 1973, figs 3, 4). Data was collected at 25 m intervals on the E-W traverse lines, with spacings occasionally reduced to 12.5 m for finer detail. The N-S base line was read at 50 m intervals.

A base station on granite at Station 0 on Line 0 was occupied at approximately 1-2 hourly intervals to provide diurnal drift correction data. As far as could be determined, all survey lines

were commenced and terminated over granite, judging by observable trends in soil and rock outcrop. As aids to interpretation, the drift-corrected data was presented in profile and contour plan formats.

Magnetic Susceptibility Implications

Magnetic susceptibilities were measured on selected samples giving: fresh basalt (W side of hill) 1500×10^{-6} c.g.s. units; relatively fresh amphibole basalt (S side of hill) 800×10^{-6} c.g.s. units; weathered amphibole basalt breccia (NW side of hill, Pit No. 4) 2000×10^{-6} c.g.s. units. A light-coloured breccia from the Brigooda pipe, similar to that at Ballogie but fresher, gave 600×10^{-6} c.g.s. units. Susceptibilities for the basalts are towards the low end of the known range for this rock type (Parasnis, 1972, table 1).

These susceptibilities give the breccia pipe a wide, low to moderate negative anomaly (trough with min. 51950 nT on line 1½ relative to surrounding granite, max. 53495 nT). Basalts produced the highest range of readings (52950-54035 nT).

Breiner, S., 1973. Applications manual for portable magnetometers. Geo Metrics, California, U.S.A. Figs 3, 4; pp. 5, 6.

Parasnis, D.S., 1972. Principles of Applied Geophysics, 2nd ed. Chapman & Hall, London. Table 1 (Volume susceptibilities), p.6.

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MAGNETOMETER SURVEY - BALLOGIE QUEENSLAND - CONTOUR PLAN

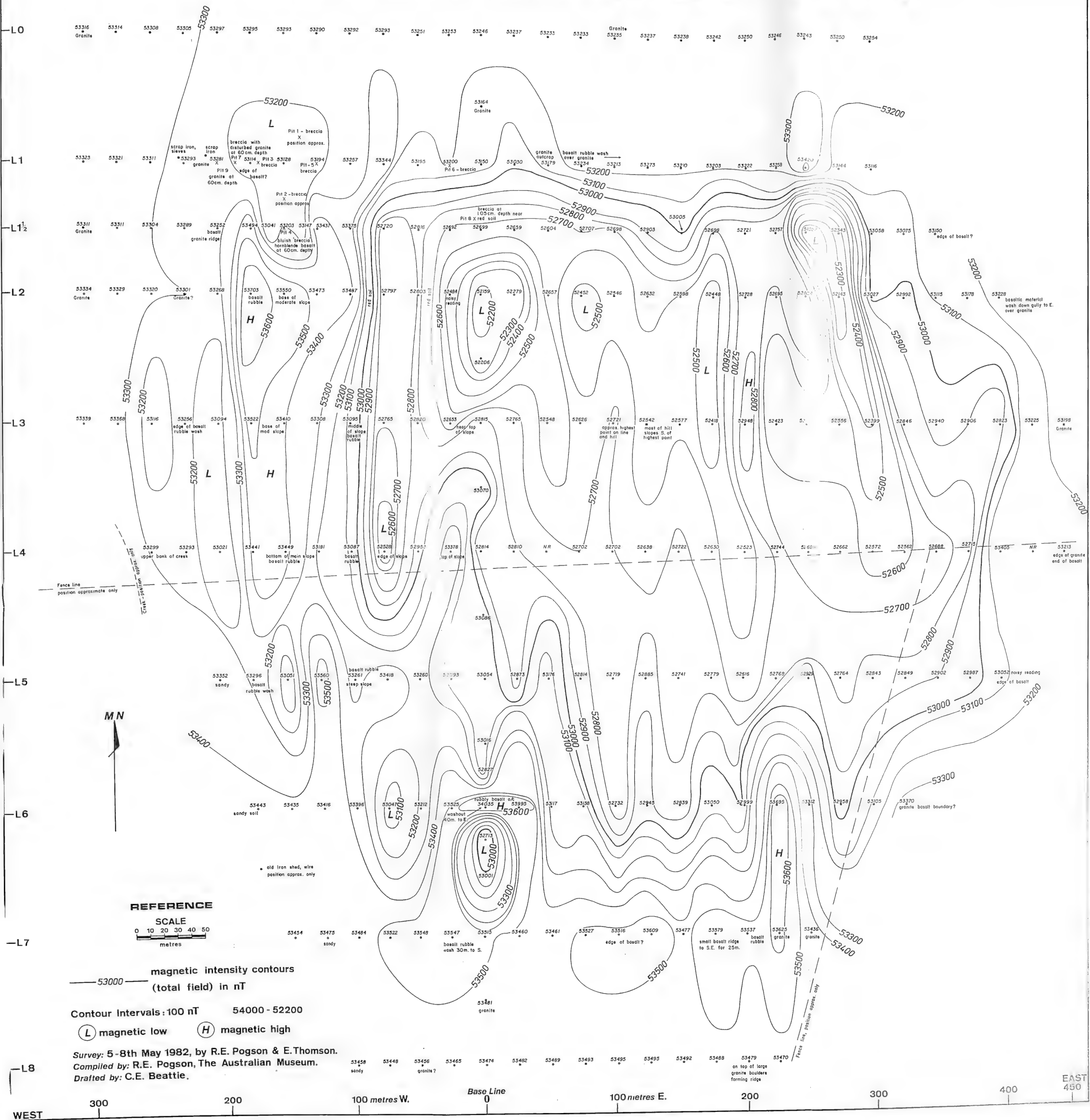
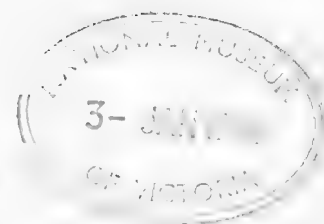


Fig. 2a. Magnetometer survey, contour map, Ballogie gem prospect.

The Taxonomy of Australian Elapid Snakes: A Review

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ABSTRACT. Published data on Australian elapid snake taxonomy are reviewed. Both classical morphological studies and relevant ecological, chromosomal and biochemical data are summarized.

Attention is focused on two major areas:

- (1) the phylogenetic relationships between Australian terrestrial elapids and other proteroglyphs; and
- (2) the interrelationships among the Australian terrestrial elapids.

From this review four key questions are identified:

- (1) Are the continentally endemic groups of terrestrial elapids confamilial?
- (2) Do the Australian elapids represent a distinct familial group?
- (3) Are the Australian elapids monophyletic or have the extant forms been derived from distinct lineages which may represent more than one invasion of the continent?
- (4) What is the precise relationship between laticaudine and hydrophiine sea snakes and the Australian elapids?

There is considerable disagreement concerning generic allocations and suprageneric relationships within the Australian proteroglyphs. Ecological, cytological and biochemical studies currently under way may be useful adjuncts to morphological information in resolving these questions.

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The combined proteroglyphous or fixed-front-fanged snakes are represented world-wide by approximately 63 genera and 245 species (Elapidae, Laticaudidae and Hydrophiidae of some authors). Of these, 16 genera and 53 species are marine forms. This group contains a large percentage of those venomous snake species dangerous to man.

This report summarizes the published classifications on the Australian elapids, including those based on morphological criteria as well as the recent biochemical and cytological work that has obvious taxonomic implications. The aim of this review is to clarify the problems still to be resolved in elapid taxonomy and provide a taxonomic baseline for future contributions. This paper provides a summary of previous taxonomic studies, but does not suggest any new taxonomic designations. Nor do I wish to offer a reassessment of characters. Consequently, I have avoided weighting characters or biasing the presentation toward any one of the classifications that have been published. The paper deals first with the question of relationships among proteroglyphous snakes world-wide, and then focuses on relationships among the Australian terrestrial proteroglyphs.

1973), the incomplete nature of most of the fossil forms, and consequent difficulty of recognizing primitive and derived character states in them (Dowling & Duellman, 1978; see also Schwaner & Dessauer, 1982).

Storr (1964) pointed out that the Elapidae (presumably referring to all terrestrial proteroglyphs) give the appearance of an "old declining group". He also commented that, with the exception of *Naja* (true cobras), all the forty or so then recognized genera formed distinct geographic groups endemic to particular continents.

The terrestrial elapids are generally considered to have been derived from a colubrid ancestor. The marine proteroglyphs are assumed either to have been derived directly from terrestrial elapid snakes or else to share a common ancestral stock with them (see Cogger, 1975a for summary). Indeed their close affinities were indicated by Underwood (1967), who gave them confamilial status with a single division between all terrestrial (subfamily Elapinae) and marine (subfamily Hydrophiinae) forms (Table 1). This was subsequently supported by Hardaway & Williams (1976) following an analysis of the costal cartilages of the ribs and modified by Underwood (1979) to include subfamily Laticaudinae. Dowling (1967) also placed all proteroglyphs in the family Elapidae but divided the family into four subfamilies: Apisthocalaminae ("stem elapids"), Elapinae ("terrestrial elapids"), Laticaudinae ("recent sea snakes"), and Hydrophiinae ("advanced sea snakes").

I. A BACKGROUND TO "ELAPID" CLASSIFICATION

Table 1 lists all genera of proteroglyphs, their common names and some relevant taxonomic comments from the literature.

The sparse fossil record of elapids commences in the upper Miocene in France and Morocco (Hoffstetter, 1962). This record, however, has been of little help in determining precise categories of snake taxa owing to the lack of critical fossils (Dowling, 1959; Marx & Rabb,

1. The Origins and Affinities of the Terrestrial Proteroglyphs

1(a). The Morphological Data

Doubt was cast on the monophyletic origin of the proteroglyph condition by the work of Bourgeois (1965) on the African Mole Viper (*Atractaspis*) and that of McDowell (1968) on the African elapid snake *Elaps* (=

Homorelaps sensu Boulenger 1896 = *Homoroselaps* as per opinion 1201 of Int. Comm. Zool. Nomenclature, 1982). Both authors attempted to demonstrate that the closest affinities of their respective forms lay with the same group of rear-fanged (opisthoglyphous) African colubrids. This would mean that the two separate venom delivery systems of the Viperidae (solenoglyphous [movable-front-fanged] snakes), to which *Atractaspis* then belonged, and the Elapidae (proteroglyphous [fixed-front-fanged] snakes), to which *Elaps* then belonged, would have arisen in parallel from a somewhat similar ancestral stock. In the most recent summaries of snake classification (Smith *et al.*, 1977; Underwood, 1979; Harding & Welch, 1980), which relied heavily on the morphological work of McDowell, *Atractaspis* has been accorded the status of a separate subfamily (Atractaspidinae) within the family Colubridae, though Branch (1981) suggested that tribal designation within the subfamily Aparallactinae may more accurately reflect its relationship. *Elaps*, the type genus for the family Elapidae, appears to be well differentiated from all other members of the Elapidae in dental and skull characters. In the light of this, McDowell (1968) adopted the generic name *Homorelaps* used by Boulenger (1896) and suggested the affinities of the genus lie with the Aparallactinae, family Colubridae, a transfer which has not been accepted by all workers (Kochva & Wollberg, 1970). A recent decision by the International Commission on Zoological Nomenclature (Opinion 1201, 1982) resulted in suppression of the name *Elaps* and validation of *Homoroselaps* for '*Elaps*' *lacteus* and *dorsalis*. Elapidae was retained as the family name.

McDowell (1970) regarded the fossorial African *Elapsoidea* as among the most primitive of existing elapids, together with *Bungarus*, *Boulengerina* and to a lesser extent *Paranaja*. Branch (1979) pointed out that the absence of both apical pits and a loreal scale, two characteristics common to all elapids, may indicate a fossorial ancestor. These characters are shared with the aparallactine colubrids of Africa, which also show a fossorial mode of life. This has led both McDowell (1970) and Branch (1979) to conclude that the aparallactines most resemble the presumed ancestral stock.

An alternative point of view regarding the origin of the proteroglyph condition was proposed by Savitsky (1978). He argued that the New World coral snakes, composed of the three genera *Micrurus* (50+ species), *Leptomicrurus* (3 species), and *Micruroides* (1 species), and making up approximately 30% of the world's terrestrial elapid fauna, represent an independent derivation of the proteroglyphous condition. He suggested that these three genera share an origin with the rear-fanged xenodontine colubrids of South America. Duellman (1979) has supported this idea by removing them to a separate family, the Micruridae. McDowell (1967, 1969a), on the other hand, had earlier placed the micrurines with a group of semifossorial Asian elapids including *Calliophis*, *Parapistacalamus*,

Maticora and the sea kraits *Laticauda*. McDowell's classification was adopted by Smith *et al.* (1977) and three tribes within the subfamily Elapinae were erected: the Elapini (= American and North Asian coral snakes), the Maticorini (= South Asiatic coral snakes) and Laticaudini (= sea kraits).

1(b). The Biochemical Data (Terrestrial Proteroglyphs)

Turning to the chemotaxonomic data, the immunological study of Cadle & Sarich (1981) refuted the classification proposed by Savitsky (1978) and Duellman (1979). Using microcomplement fixation analysis (MC'F) Cadle and Sarich (1981) demonstrated a closer relationship between the micrurines, the Asian elapids *Ophiophagus* and *Bungarus*, the Australian elapid *Austrelaps* and the sea kraits *Laticauda*, on the one hand, than between the micrurines and any of the xenodontine colubrids or hydrophiine sea snakes on the other. They claimed that their data unequivocally placed the micrurines "on a common lineage with Asian and Australian terrestrial elapids and with the sea snakes". However, as it stands their data neither supported nor refuted the association of micrurines specifically with *Laticauda* as proposed by McDowell. In a further immunological study (Cadle & Gorman, 1981) no strong association was found between *Micrurus* and *Laticauda*. Instead, four major lineages of elapid genera were identified: (1) hydrophiine sea snakes, (2) *Laticauda*, (3) New World coral snakes and (4) one or more lineages including *Demansia* (Australian), *Bungarus* and *Ophiophagus* (Asian) which were close to none of the reference antisera they studied. Moreover, *Demansia* was clearly distinguishable from all other Australian elapids examined by these authors.

Cadle & Gorman (1981) pointed out that neither their study nor that of Cadle & Sarich (1981) included either Old World coral snakes or African elapids. Consequently many of the relationships suggested by McDowell could not be tested, nor could the relationships of the Australian elapids exclusive of *Demansia* be elucidated.

The recent MC'F work of Mao *et al.* (1983) is in concordance with the findings of Cadle & Gorman (1981) in that they too found no close affinity between *Micrurus* and *Laticauda*. The immunological distance units (IDU's) for *Micrurus* when tested along with other elapid genera against the four antisera (*Pseudonaja*, *Bungarus*, *Hydrophis* and *Laticauda*) were quite close to those obtained for *Bungarus* and *Elapsoidea* with the same four antisera, leading Mao *et al.* to agree with Cadle & Sarich's (1981) placement of *Micrurus* in Elapinae. Their report also confirmed the distinctiveness of *Demansia* from other Australian elapids. They supported the placement of the Australian elapids in the subfamily Acanthophinae by Dowling & Duellman (1978), emphasizing their distinctness from Asian and African elapids. Mao *et al.* (1983) reported an unusual character in the albumin of *Naja*. They suggested that the *Naja* albumin either is widely divergent from other elapids or has evolved at a much faster rate.

Cadle (in press) recently utilized the MC'F technique to test the hypothesis of independent origin of the proteroglyph condition from colubrid stock in micrurines and *Atractaspis*. His interpretation of these data refuted the hypothesis of affinity of either of these groups with colubrids and strongly supported the relationship of micrurines to elapids. He was unable to place *Atractaspis* unambiguously with either the elapids or viperids and suggested it may represent an independent lineage.

1(c). *Dendroaspis*—A Distinctive Elapid?

Among the African elapids the mambas (*Dendroaspis*) can be distinguished from all other forms on the basis of the morphology of the maxilla. In his classic work on reptilian osteology, Romer (1956) gave the genus separate subfamilial status (Dendroaspinæ) on the basis of this character. Dowling (1959) found this to be an unacceptable criterion for subfamilial distinction. It is interesting to observe that Underwood (1967) described the skull of *Dendroaspis* as differing from all other African elapids in lacking both choanal and maxillary processes on the palatine bones. The Australasian elapids also lack the choanal process and, with the exception of *Ogmodon* (Fiji), lack the maxillary process as well (McDowell, 1970). McDowell further elaborated upon the distinctiveness of the dentition and palatine kinesis in *Dendroaspis* but did not remove them taxonomically from other African elapids.

More recently several authors have used a variety of biochemical characters to infer relationships. Saint Girons & Detrait (1980), for example, have analysed *Dendroaspis* venom in terms of per cent common antigens, immunodiffusion, and immunoelectrophoretic comparisons against African (*Naja* and *Hemachatus*), Australian (*Austrelaps* and *Pseudechis*) and Asian (*Naja* and *Bungarus*) elapids. They found only minor similarities between the venom of *Dendroaspis* and all the other genera examined. Saint Girons & Detrait argue that, when they exist, antigenic similarities reflect phylogenetic and not functional affinities.

2. The Origins and Affinities of the Marine Proteroglyphs

2(a). The Morphological Data

An affinity between the sea snakes and the terrestrial proteroglyphs has long been suspected. In a series of studies on proteroglyphs McDowell (1967, 1968, 1969a, 1969b, 1970, 1972, 1974) analysed a suite of morphological characters, including the osteology of the skull, dentition, venom gland musculature and hemipenial structure. Two important points emerged from his analysis. First, the sea kraits of the genus *Laticauda* were held to have originated quite separately from other sea snakes, which collectively form the hydrophiids. Second, the structure of the palatine bone and associated processes was held to imply a taxonomic dichotomy based on the functional kinesis of these

structures among proteroglyphs. McDowell termed the two groups "palatine erectors" and "palatine draggers". Most terrestrial elapids fall into the category of "palatine erectors" with the notable exception of the Australian elapid snakes which, like the hydrophiine sea snakes, are "palatine draggers" (McDowell, 1970). This information led Smith *et al.* (1977) to propose a rather controversial classification in which the Australian elapids are transferred from the family Elapidae to a subfamily Oxyuraninae within the Hydrophiidae. The laticaudine sea snakes, formerly a subfamily of the Hydrophiidae, are placed in the tribe Laticaudini, subfamily Elapinae, together with North Asiatic and American coral snakes. The remaining elapid subfamily, the Bungarinae, then contains two tribes which include all Asiatic and African terrestrial elapids (see Tables 1 and 2).

McDowell considered the laticaudine sea snakes no more than a divergent line within the terrestrial elapids while Voris (1969) concluded, in agreement with Smith (1926), that *Laticauda* is the most primitive of extant sea snakes though sharing a common origin with the more specialized forms (see Cogger, 1975a). Voris (1977) subsequently reported on a multivariate analysis of 43 characters and concluded that: "*Laticauda* do not stand on a character-by-character basis between the terrestrial elapids and the other sea snakes . . . They (the *Laticauda*) are very distinct from all other sea snakes and either represent an independent evolutionary line or a very early separation from all other sea snakes. They are by far the most primitive sea snakes and possess many elapid character states". These later views of Voris appear to bring his assessment in closer line to McDowell's than earlier indicated.

Smith (1931) drew attention to the monotypic genus *Ephalophis* which he considered primitive and perhaps intermediate between the laticaudine and hydrophiine sea snakes. McDowell (1969b) placed *Hydrophis merti* in the genus *Ephalophis* and suggested that through it the hydrophiines were derived from the Australian elapids of the "*Demansia*" group and specifically *Drepanodontis* (= *Hemiaspis*) and *Rhinoplocephalus* (McDowell, 1967, 1972, 1974). McDowell also divided the hydrophiine sea snakes into three groups based on scalation, vertebral anatomy, venom gland musculature and skull morphology, namely:

- (1) the *Hydrelaps* group including only the distinctive, and in many respects primitive, genus *Hydrelaps*;
- (2) the *Aipysurus* group with *Ephalophis* being the most primitive genus in this group but also including *Aipysurus* and the very specialized *Emydocephalus* which feeds exclusively on fish eggs;
- (3) the most advanced, *Hydrophis* group containing most of the remaining sea snake genera (see McDowell, 1967, 1970 for list of generic changes).

This differed radically from Smith's (1926) concept of the family Hydrophiidae, which he believed should contain subfamily Laticaudinae, including *Laticauda*, *Aipysurus* and *Emydocephalus*, and the subfamily

Hydrophiinae, including *Hydrophis* and all other genera.

Voris (1977) agreed with the classification of McDowell (1967, 1970), who pointed out the primitive status of *Hydrelaps*, though Voris placed *Ephalophis* with *Hydrelaps* in a separate group instead of including it among the *Aipysurus* group. Voris also points to *Hydrophis* (= *Disteira* of McDowell, 1972) *kingi*, *H. (D.) major*, *Kerilia jerdoni* and *Thalassophis* as "relatively primitive" and possibly divergent from the main and more recent *Hydrophis* stock.

Cogger (1975a) reduced McDowell's (1972) genus *Disteira* substantially by retaining the species *schistosa* and *stokesii* in the genera *Enhydrina* and *Astrotia* respectively, a move adopted by all subsequent authors.

In a brief review of the sea snakes, Burger & Natsuno (1974) reassessed the available data and analysed internal morphological features. They drew attention again to *Ephalophis (Hydrophis) mertoni* and, because of the location of the heart, lack of the vestigial left lung seen in *E. greyi*, and dorsal scale differences, *E. mertoni* was considered more advanced than *E. greyi* and a new genus *Parahydrophis* was erected to include only *P. mertoni*. A new subfamily Ephalophiinae was erected to include five genera which the authors divided into three groups: (1) "*Hydrelaps* group" for *Hydrelaps* only; (2) "*Ephalophis* group" for *Ephalophis* and *Parahydrophis*, with *Ephalophis* selected as the type genus of the subfamily; and (3) "*Aipysurus* group" for *Aipysurus* and *Emydocephalus*. This bears an obvious resemblance to the grouping of genera suggested by McDowell except for the splitting of the *Aipysurus* group of McDowell and the elevation of these three groups to form a subfamilial assemblage. The other genera remained in the Hydrophiinae, though *Disteira* (McDowell, 1972, and *sensu lato* Cogger, 1975a) has been put back into *Hydrophis*. Burger and Natsuno also reaffirmed the distinction between *Laticauda* and the hydrophiid sea snakes and emphasized it by placing them in separate families, resurrecting the Laticaudidae for the sea kraits and the Hydrophiidae for all other sea snakes.

2(b). The Biochemical Data (Marine Proteroglyphs)

Turning to the published biochemical data on this group, Mao *et al.* (1977) have examined the structural affinities of the transferrins of *Hydrophis*, *Lapemis*, *Pelamis* ("Hydrophis group" of McDowell), *Aipysurus*, *Emydocephalus* (the "*Aipysurus* group" of McDowell), *Laticauda*, *Naja* and *Bungarus* (the Elapidae of McDowell), using the MC'F technique. Their interpretation of the data agrees well with McDowell's (1972) classification with two exceptions: (1) the indices of dissimilarity suggest that the sea snakes, here including the *Laticauda*, have diverged from Asian terrestrial elapids at the familial level (Australian genera were not examined), and (2) the two-way reciprocal titrations between *Laticauda* and *Hydrophis* demonstrate closer affinities between the genera than the morphological

criteria indicated, though this does not seem to be supported by Cadle and Gorman's MC'F work (1981).

The data of Mao *et al.* (1977) are broadly compatible with the immunoelectrophoretic data of Minton & da Costa (1975). The latter authors supported many of McDowell's associations with the exception that they found *Emydocephalus* to be more distinct from *Aipysurus* serologically than it is morphologically. Minton & da Costa also suggested that the sea snakes represent "a homogeneous group closely related to the Australian elapids". From their data *Laticauda* showed greater reactivity to the Australian elapid antisera of *Denisonia* (= *Austrelaps* in this instance) than did *Lapemis* and *Hydrophis*. The sample species, however, did not allow the authors to test McDowell's theory of an Asian rather than an Australian origin of *Laticauda* or to determine its relation to the family Elapidae. In a subsequent review of his own work Minton (1981; see also Minton, 1978) concluded that the elapid stocks have probably been distinct since the Miocene though the origin and affinities of the family remain unknown. Minton further describes the Hydrophiidae as containing two stocks, with *Laticauda* being distinct. The venom analysis of Coulter *et al.* (1981) found a close relationship between Australian elapids and sea snakes, in agreement with Minton & da Costa (1975), but did not find a close relationship between 'exotic' terrestrial elapid venom (here presumably referring to African and Asian elapids) and Australian venoms.

As mentioned above, the MC'F work of Cadle & Gorman (1981), included a comparison of sea snakes with both Asiatic and Australian elapids and indicated that sea snakes comprise three groups similar to McDowell's classification (i.e. hydrophiids, aipysurids and laticaudids). Though the question of a single versus a multiple origin of sea snakes could not be answered by the immunological data, it appeared that, with the exception of *Demansia psammophis*, the Australian forms are close to both *Hydrophis* and *Laticauda*.

The more recent MC'F work of Mao *et al.* (1983) utilized albumin and from these data the authors suggested *Laticauda* is closely related to hydrophiines, thus supporting their earlier transferrin data (Mao *et al.*, 1977). They also found the sea snakes to be closer to Australasian elapids than to the elapids on other continents.

2(c). The Chromosomal Data (Marine Proteroglyphs)

Gorman (1981) has reviewed published data on sea snake karyology. He reported gross karyotypic data for three species of laticaudine sea snakes and reviewed chromosomal data for 18 species of elapids (excluding those published by De Smet, 1978, and Gutiérrez & Bolaños, 1979). It is apparent from this study that a considerable amount of gross karyotypic data is available on sea snakes. This is due largely to the efforts of Singh (1972a,b, 1974). Sea snakes reported thus far vary in diploid number from 32 to 40 with some hydrophiids having undergone rearrangements of the W sex chromosome, giving rise to ZW₁W₂ females. It

is also interesting to note that all hydrophiids karyotyped thus far display a secondary constriction on pair one while no such constriction has been mentioned in *Laticauda*. No karyotypic data have been published for any of the species making up the *Aipysurus* group of McDowell, which is thought to comprise the primitive and intermediate hydrophiids. Gorman (1981) concluded that most of the chromosomal variation observed in sea snakes can be attributed to centric fission and sex chromosome rearrangements with general conservation of macrochromosomes. On the basis of this and the similarity of gross karyotype ($2n = 34; 14 M + 20 m$) between one of the three *Laticauda* species he reported and *Notechis scutatus*, the only Australian terrestrial elapid for which chromosomal data are currently available (Shine & Bull, 1977), Gorman suggested that these two genera share a primitive karyotype. Indeed, Gorman (1981) proposed that this karyotype may represent the ancestral condition for the elapid radiation. Such an assumption would seem highly tenuous considering the lack of chromosome data on the remaining 24 genera of Australian terrestrial elapids.

3. A Summary of Proteroglyph Relationships

The one thing that should be apparent from the foregoing discussion is the inability of taxonomists to arrive at any unanimity. This stems directly from the difficulty of defining primitive and derived character states.

The affinities of proteroglyphs to their possible colubrid ancestors remain poorly understood. Three distinct colubrid groups have been suggested as showing ancestral relationship to various elapid stocks. On morphological criteria aparallactine colubrids are suggested to resemble some African elapids (McDowell, 1970; Branch, 1979) while other workers have suggested that xenodontine colubrids resemble the precursor of the micrurine elapids (Savitsky, 1978). Minton & da Costa (1975) have cautiously suggested an unexpected relationship between natricine colubrids and sea snakes on the basis of serological studies. Anthony & Guibé (1951, 1952) have even suggested a polyphyletic origin, with some elapids being derived from the boids *Bolyeria* and *Casarea*. Cadle, however, insisted that molecular data do not support a close affinity between these elapid and colubrid groups.

A greater consensus of opinion has prevailed on the groupings and relationships of sea snakes. Both morphological and biochemical data have suggested a close relationship between Australian terrestrial proteroglyphs and hydrophiid sea snakes. Likewise, most authors agreed on the general division of hydrophiid sea snakes into three groups, yet there is little agreement upon the precise relationship of *Laticauda*.

From the confused taxonomic picture three key questions remain to be resolved at the familial level, namely: (1) Are the continentally endemic groups of terrestrial elapids confamilial (as suggested by Underwood, 1967) or, if not, do the Australian elapids

represent a distinct familial group? (This possibility was also referred to by Underwood, 1967, in reference to the work of Storr, 1964; Dowling & Duellman, 1978, placed them in a separate subfamily Acanthophinae.), (2) Are Australian elapids a monophyletic group?, and (3) What is the precise relationship between the laticaudid and hydrophiid sea snakes and the Australian elapids, and is there evidence to demonstrate an independent origin of hydrophiid and laticaudid sea snakes?

II. TAXONOMIC RELATIONSHIPS WITHIN THE AUSTRALIAN TERRESTRIAL ELAPID SNAKES

Two of the zoogeographic works which included reference to the Australian elapid fauna were those of Storr (1964) and Cogger & Heatwole (1980). Both studies pointed out the high degree of endemism in Australian elapids. Cogger & Heatwole (1980), for example, found that 94% of all Australian elapids (approx. 25 genera and 63+ species) are endemic, with the remainder being shared with New Guinea. Only one species of Death Adder (*Acanthophis*) extends to the islands beyond New Guinea. Such a high degree of generic endemism among reptiles in Australia is exceeded only by the pygopodid lizards.

Storr (1964) suggested that Australian elapids are derived from early colubrids, probably originating in Asia and invading the Australian continent at a time when more primitive colubrids were waning and before the modern colubrid radiation (see also Cogger & Heatwole, 1980). Storr interpreted the high degree of continental endemism to imply that the Elapidae are an old, declining group. The fossil record provides no information on the age of the elapid radiation in Australia, although Cogger & Heatwole (1980) suggest "the major adaptive radiations within Australia in such groups as the elapid snakes, diplodactyline geckoes, the endemic family Pygopodidae and major segments of the lizard families Agamidae, Varanidae and Scincidae are almost certainly derived from elements which arrived no later than the mid-Tertiary. These indigenous radiations, however, apparently proceeded with little or no modification by later migrations of the same families until well into the Quaternary, suggesting that Australia's reptile fauna evolved in virtual isolation between at least mid-Tertiary and the beginning of the Quaternary (a period of 30–35 million years) when a new series of migrations from Asia commenced".

1. The Classifications since Günther (1858)

The taxonomic interrelations of the Australian elapid snakes have long been a question for debate. Before attempting to outline the problems I would like to draw

the reader's attention to the distinction between that portion of the literature that reflects a failure to apply the rules of zoological nomenclature and those problems which actually reflect a difference between authors' concepts of the relationships of organisms. It is cases of the latter type that will be discussed in detail here. To assist the reader with nomenclatural problems of the former type, Table 3 provides a list of all generic and specific names that have been applied to Australian terrestrial and marine proteroglyphs and their currently used synonyms. These data were derived largely from the checklist of Cogger *et al.* (1983); for a more detailed synonymy and justification of some of the taxonomic allocations listed I refer the reader to that work.

Table 2 provides an alphabetic list of currently recognized species cross-referenced to the classifications of the eight major workers since Günther (1858). This table demonstrates that many species have been assigned to four or more genera over the years. Likewise currently accepted generic divisions (Cogger, 1975b, 1979) may contain species that were at one time thought to be related to four different generic groups (see *Simoselaps* Table 2). The opinions of Cogger (1975b, 1979) have been used as a taxonomic guideline in these comparisons, because they represent the most recent and complete review of the Australian elapids and more fully adhere to the basic guidelines of the International Code for Zoological Nomenclature. Table 2 also includes recent synonymies and lists species described since Cogger's 1979 publication.

2. The Morphological Data

What is immediately apparent from Table 2 is the variety of classifications that can be derived from the same morphological data base. This lack of agreement among taxonomists again reflects an inability to distinguish between primitive and derived character states. Until McDowell's contribution on hemipenial morphology and venom gland musculature all workers relied essentially upon the same morphological data set, consisting largely of scale and skeletal characteristics.

A cursory examination of Table 2 indicates that many authors have used the work of Boulenger (1896) as a taxonomic guide to the Australian elapid fauna. Indeed, the subsequent studies of Worrell (1955, 1960, 1961, 1963), based largely on skull morphology, represented the first major shift since Boulenger's early work. Prior to Worrell over 50% of Australian elapid species were assigned to two large genera *Denisonia* and *Diemenia* (*Demansia*). A chronological treatment of the taxonomic changes to these and other major genera will serve to illustrate the alterations to elapid classification outlined in the table.

2(a). Taxonomic changes to Boulenger's *Denisonia*

As mentioned above, Worrell's work in the early 1960's was the first major deviation from the classification of Boulenger (1896). Worrell attempted to reassign Australian elapid species into groups more

closely reflecting similarities in cranial and dental characteristics and to a lesser extent in external morphology. This resulted in his dividing the large genus *Denisonia* into a series of genera including: *Austrelaps* for *D. superba* and *D. signata*; *Cryptophis* for *D. pallidiceps* (type species), *D. nigrescens*, *D. flagellum* and *D. dwyeri*; *Drepanodontis* for *damelii*; *Drysdalia* for *coronata*, *coronoides* and *mastersi*; *Parasuta* for *gouldii* and *nigrostriatus*; *Suta* for *suta*; and *Unechis* for *carpentariae*. The genus *Denisonia* thus was left with only four species: *devisii*, *fasciata*, *maculata* and *punctata*.

As with any major change in taxonomic convention, Worrell's efforts elicited varied reactions. His dismemberment of *Denisonia* proved to be his most controversial taxonomic move. While most workers to date have accepted the use of *Austrelaps* (for *superba* but not *signata*) and *Drysdalia* they show differing attitudes toward the remaining genera. Brongersma and Knaap-Van Meeuwen (1964) for example, strongly opposed the splitting of *Denisonia* in their description of *D. boschmai* (later synonymized with *S. (Unechis) carpentariae* by Parker, 1972. It has been found that the holotype of *carpentariae* is conspecific with *Suta suta* and Cogger *et al.* (1983) have applied the next available name, *boschmai*, for *carpentariae* of authors). Based on a comparison with Worrell's figures and referring to the data of Kinghorn (1920), Brongersma and Knaap-Van Meeuwen (1964) demonstrated variation in two of the characters Worrell had used to define *Cryptophis*. As the diagnostic characters did not hold up they thus rejected the generic proposals of Worrell's division of *Denisonia*. Coventry (1971) avoided any mention of the generic classification of Worrell in his treatment of the black-headed *Denisonia* of Victoria, but stated that this group was polyphyletic and that similarities were due to convergence.

The next investigator after Worrell to assess the relationships of Australian elapids was McDowell (1967). In a study of the New Guinea species of *Aspidomorphus* and their relatives he examined many Australian species and attempted to group them according to hemipenial morphology and the structure of the adductor externus superficialis muscle surrounding the venom gland. In the Australasian elapid snakes, with the exception of *Elapognathus*, *Laticauda* and *Parapistocalamus*, the hemipenis lacks the alveolar calyces which are seen in many African and Asian forms (e.g. *Naja* and *Bungarus*).

The absence can, however, be explained in two ways, which in terms of *Denisonia* resulted in the separation of *D. devisii* and *D. maculata* into one group while McDowell placed in another group the remainder of Boulenger's *Denisonia*.

McDowell's (1967) classification of species according to the morphology of the adductor externus superficialis muscle resulted in somewhat different groupings (see Section 2[f]). All of the four categories recognized by McDowell (1967) contained species formerly referred to *Denisonia* by Boulenger. Thus, the "*Glyphodon* group"

contained *Cryptophis pallidiceps*, *C. nigrescens* and *Drysdalia coronoides* of Worrell. The "Oxyuranus group" contained *Denisonia maculata*, *D. devisii* and *Drysdalia coronata*. The "Pseudechis group" contained *Parasuta gouldii*, *P. nigrostriata*, *Unechis carpentariae*, *Denisonia boschmai*, *Austrelaps superbus*, *Cryptophis flagellum* and *Denisonia punctata* of Worrell. The fourth group, the "Demansia group" contained *Drepanodontis daemeli* and *Austrelaps signata*. This classification further divided every genus Worrell had erected from Boulenger's *Denisonia*, including the four species which he retained in *Denisonia*.

McDowell (1967), stated that, despite cases of parallelism and convergence, venom gland musculature "shows better correlation with other features than does any other single character". In Worrell's division of *Denisonia*, McDowell found fault in the placement of *flagellum* with *pallidiceps* and *nigrescens* in *Cryptophis* and suggested its association with *gouldii*, the type of Worrell's *Parasuta*. He indicated a further anomaly in the inclusion of *Denisonia punctata* with the remaining species of *Denisonia* as restricted by Worrell. The venom gland musculature of *D. punctata* is more like that of the genera *Suta*, *Parasuta* and *Unechis* of Worrell; and this is in agreement with data on hemipenial morphology. Shine (1983b) demonstrated that the feeding strategies and food preferences of *D. fasciata* and *D. punctata* differ from those of *D. maculata* and *D. devisii*. In a publication defining the "Pseudechis group" McDowell (1970: see below) moved to include all those species of Worrell in the genus *Suta*, thus resulting in *S. flagellum*, *S. punctata*, *S. fasciata*, *S. carpentariae* (= *boschmai*), *S. monachus* and *S. gouldii*. This move was adopted by Parker (1972) in his revision of *S. carpentariae* (= *boschmai*) and *S. nigrostriata* in Australia and New Guinea. Subsequent authors, however, have not accepted McDowell's use of *Suta*.

Cogger (1975b, 1979) attempted to provide a general consensus of the relationships of species in this large group by critically applying the rules of taxonomic nomenclature to the morphological studies of McDowell (1967, 1969, 1970). In this process some of the generic names of Worrell were retained while species formerly allocated to *Parasuta* and *Drepanodontis* were referred to other genera (see Table 3 and below). In his report McDowell (1967) pointed out that *signata*, placed in *Austrelaps* by Worrell (1963), could be identified as *Drepanodontis* using Worrell's (1961) key. In fact the venom gland musculature, dentition and skull morphology of *signata* were much like those of *Drepanodontis daemeli*, so McDowell placed the two species together in *Drepanodontis*. Cogger (1975b) followed this but adopted the earlier name *Hemiaspis* for the two species. Thus McDowell's groupings based on his new morphological data set were reflected in Cogger's (1975b) classification though *Unechis* was used for *carpentariae* (= *boschmai*, see Cogger et al., 1983), *gouldii*, *nigrostriatus*, and *flagellum*; and *Cryptophis* was retained for *pallidiceps* and *nigrescens*. *Austrelaps* was restricted to

superbus while *signata* was placed along with *daemeli* (*daemeli*) in the genus *Hemiaspis*. Cogger recognized Worrell's *Drysdalia*.

In contrast to the classifications of McDowell and Cogger some authors (Storr, 1981b; Coventry, 1971) have preferred to treat the problematic *Denisonia* in terms of species groups within a large genus. Though the distinction between species groups and genera may simply be a matter of semantics the definition of these species groups has suffered from the practice of restricting reports to species and specimens whose ranges coincide with political or State boundaries. As a consequence, no complete treatment of the species groups involved has been produced. The reviews of the "*Denisonia (Unechis) gouldii*" species group in Victoria by Coventry (1971) and in Western Australia by Storr (1964, 1981b) resulted in redefining *gouldii* (restricted to W.A.) and *dwyeri* (distributed in Victoria, N.S.W. and Queensland) and in describing several new forms from Western Australia.

The most recent change to *Denisonia* (*sensu* Boulenger) was that of Storr (1982) who suggested the transfer of the species of *Drysdalia* and *Austrelaps* to the genus *Notechis* (see below).

2(b). Taxonomic Changes to Boulenger's *Diemenia* (*Demansia*)

Unlike his treatment of *Denisonia*, Worrell's division of Boulenger's *Diemenia* has stood the test of time. Using skull characteristics Worrell divided *Diemenia* into the whip snakes *Demansia* and the brown snakes *Pseudonaja*. Though a number of additional species are currently recognized in *Demansia* based largely on colour pattern differences, both genera appear well defined. On the basis of venom gland musculature McDowell (1967) fully supported Worrell's separation of the genus *Pseudonaja* from *Demansia*. This generic division was recognized by all subsequent workers.

2(c). Taxonomic Changes to *Pseudelaps*, *Furina* and *Glyphodon*

Affinities between the species Boulenger assigned to these three genera have long been recognized, but generic divisions within this complex continue to be debated. Worrell divided the genus *Pseudelaps* as used by Boulenger (1896) by reviving *Brachysoma* for *diadema*, erecting *Lunelaps* for *christianus* [sic], recognizing the genus *Aspidomorphus* in Australia for *squamulosus* alone, placing *harrietae* in the genus *Glyphodon* and resurrecting *Cacophis* for *kreffti*. Boulenger recognized in *Furina* only *F. occipitalis* and *F. calonotus*, whereas Worrell described the new genera *Narophis* for *bimaculata* and *Melwardia* for *calonotus* and *minima*. (*F. occipitalis* is now a synonym for *Vermicella annulata*.)

In his report McDowell demonstrated that *christianus* and *diadema* were congeneric. As *Brachysoma* was a junior homonym and therefore unavailable, McDowell placed the two species in *Furina*. This move eliminated *Lunelaps* of Worrell. McDowell states "*Furina* is related

to *Glyphodon* rather than to *Aspidomorphus* (here presumably including *Cacophis*) or *Demansia*". *Furina christianus* [sic] was included in *F. diadema* by Cogger & Lindner (1974). In a recent review of the genus *Furina* in Western Australia, Storr (1981) considered specimens previously allocated to *F. christianus* to be distinct from *diadema*, and resurrected the name *F. ornata*. Storr (1981) also included in *Furina*, however, two species of the genus *Glyphodon* (*barnardi* and *tristis*) and one species of *Simoselaps* (*warro*) though no reassessment of these species was offered. It should be noted that Shine (1981) suggested that *Furina* and *Glyphodon* are ecologically similar.

McDowell (1967) also analysed the species *kreffti*, *harrietae* and *squamulosus*, which Worrell had placed in *Cacophis*, *Glyphodon* and *Aspidomorphus* respectively, and, on the basis of hemipenial morphology, dentition, head scutellation and colour, combined them all in *Cacophis*.

2(d). Taxonomic Changes to *Vermicella* and *Simoselaps*

One of the most prolific contributors to Australian elapid taxonomy has been Storr. In his 1967 work on *Vermicella* he combined species which Worrell (1960, 1961, 1963) and Kinghorn (1955, 1956) had earlier referred to the genera *Narophis*, *Melwardia*, *Brachyuropsis*, *Rhynchoelaps*, *Rhinelaps* and *Vermicella*. He also described several new forms. In a subsequent revision of the genus Storr (1978) elevated to species status three taxa—*bertholdi*, *littoralis*, and *anomala*—previously considered as subspecies of *V. bertholdi*, and also reinstated *V. approximans* and *M. minima* as full species. Having thus disposed of all other *Simoselaps* species (*sensu* Cogger, 1975b), Storr (1979) left *warro* in its original combination, *Cacophis warro*. He subsequently chose to place it in the genus *Furina* (see above, Storr, 1981c).

In his detailed analysis of the New Guinean genus *Toxicocalamus* McDowell (1969a) showed that *Vermicella* was most closely related to the Australian genera *Brachyuropsis*, *Melwardia*, *Narophis*, *Rhinelaps* and *Rhynchoelaps* of Worrell (1963). McDowell recognized and agreed with Storr's (1967) move to group these genera together but excluded *annulata*. Since *annulata* is the type species for *Vermicella*, McDowell restricted the genus to *annulata* and proposed *Rhynchoelaps* Jan, 1758 as the next available name (type *Elaps bertholdi* Jan) for Storr's remaining species. The *Rhynchoelaps* group of McDowell (1969a) therefore contained two genera: *Rhynchoelaps*, including the *Vermicella* of Storr (1967) (except for *V. annulata* and presumably *multifasciata*), and the genus *Toxicocalamus* as redefined. Cogger, (1975b, 1979) restricted *Vermicella* to *V. annulata* and *V. multifasciata* following McDowell (1969d), but divided the species assigned to *Rhynchoelaps* by McDowell between *Neelaps* (*bimaculata* and *calonota*) and *Simoselaps* (all other species; Cogger regarded *Rhynchoelaps* as a *nomen nudum* and used *Simoselaps* as the next available name).

In a recent ecological study Shine (in press) follows Cogger's (1975b, 1979) use of the genera *Simoselaps* and *Neelaps* but recognizes five species groups based on feeding habits, structure and scalation of the snout and dentition. The two latter characters Shine correlates with the first. Within the two genera Shine defines the following five distinct "species groups". (1) *Neelaps bimaculatus* and *N. calonota*, both saurophagous; (2) the "*Simoselaps bertholdi* group", including *S. bertholdi*, *S. anomala*, *S. littoralis* and *S. minima*. All are saurophagous and lack the exaggerated shovel-like snout of some other species as well as the dentition adaptations; (3) the "*S. semifasciatus* group", of *S. semifasciatus*, *S. s. roperi*, *S. approximans* and *S. incinctus*. These species have a sharply upturned angular snout and are exclusively oophagous. *S. semifasciatus* possesses a single enlarged triangular tooth at the back of the maxilla; (4) *Simoselaps australis* and *S. fasciolatus*, which Shine states may not be closely related, but resemble *S. semifasciatus*; only *S. australis* shares the angular snout. Both are saurophagous and oophagous; (5) *S. warro*, which Shine, following Storr (1979), regards as being so aberrant that it is only doubtfully included in this genus (see above for Storr's assignments of this species). Shine also notes that *S. warro* resembles the "*S. bertholdi* group" in being saurophagous and lacking the modifications of the other species.

2(e). Additional Taxonomic Changes to Australian Elapids

The genera of larger Australian elapid snakes have remained relatively stable since the "dissection" by Glauert (1948), Worrell (1963) and Kinghorn (1921) of the tiger snakes (*Notechis*) into a variety of subspecies, and the recognition of *Austrelaps* and *Pseudonaja*. Most workers recognize that some species of *Pseudonaja* may be composite (Cogger, 1979; Gillam, 1979). The review of the "black snakes" of the genus *Pseudechis* by Mackay (1955) resulted in synonymizing the species into the forms recognized today. In a recent comprehensive study of the Taipan, *Oxyuranus scutellatus*, and the Small-scaled Snake, *Parademansia microlepidota*, Covacevich *et al.* (1981) analysed scalation, skull morphology, dentition, hemipenial anatomy and karyotypes, concluding that these two species are congeneric and referable to *Oxyuranus*.

Apart from these few assessments of species, however, the intra- and intergeneric relationships remain poorly understood. McDowell (1970) associated *Pseudechis* and *Austrelaps*. The genus *Pseudechis* in Western Australia has recently been reviewed by Smith (1982), with the description of a new species, *P. butleri*. Rawlinson (1969) reexamined the monotypic genus *Austrelaps* and several species are likely to be recognized. White (1981) recognized the Adelaide Hills form as distinct, but refrained from naming it. McDowell (1967) reported an unexpected resemblance between *Drysdalia coronata* and the genera *Notechis*, *Tropidechis* and *Oxyuranus*. Indeed, he could find no

internal character separating *D. coronata* and *Notechis*. McDowell (1967) indicated *D. coronata* may merit generic distinction. Shine (1981) pointed out that *coronata* is more similar to *Notechis* in its dietary preferences than are the other *Drysdalia* species. Shine and Charles (1983) suggested a close relationship between *Notechis* and *Tropidechis*, based on a review of the morphological, ecological, behavioural and cytological data. Storr (1982) has recently discussed similarities between *D. coronata* and *Notechis* and subsequently placed all *Drysdalia*, *Austrelaps*, *Elapognathus* and *Echiopsis* in *Notechis*. He did not consider *Tropidechis*. The review of *Drysdalia* by Coventry and Rawlinson (1980) resulted in the separation of *D. rhodogaster* from *D. mastersi*. Storr (1981a) reviewed the death adders (*Acanthophis*) of Western Australia and resurrected a third species, *A. praelongus*.

2(f). The Intergeneric Relationships Proposed by McDowell

While all the preceding taxonomic changes deal with the definition and allocation of species to genera, the only worker who has attempted to group related genera is McDowell. Because McDowell provided a new data set and examined a wide variety of elapid species his findings influenced both the species groupings discussed above, and intergeneric relationships. His groupings, therefore, bear repeating here.

The hemipenial morphology reported by McDowell (1967) yielded the following two groups:

—Group 1, consisting of Boulenger's *Denisonia* (*Austrelaps*, *Drysdalia*, *Cryptophis*, *Hemiaspis*, *Suta* and *Unechis* of Cogger, 1975b) and *Demansia*, *Pseudechis*, *Pseudonaja* (except *P. guttata*), *Brachyaspis* (= *Echiopsis* of Cogger, 1975b), *Oxyuranus*, *Ogmodon*, *Hydrelaps* (sea snake), and *Aspidomorphus* sensu stricto; and

—Group 2, the "Glyphodon Series", showing odd resemblance to *Ophiophagus* and including *Denisonia maculata* and *devisii*, *Acanthophis*, *Hoplocephalus*, *Glyphodon*, and Australian snakes then assigned to *Aspidomorphus* (= *Cacophis* and *Furina* of Cogger).

The groupings based on venom gland musculature were as follows: (names with asterisks have been changed to accord with Cogger, 1975b; for original names see Table 2):

—In Group 1, the "Glyphodon type" of adductor externus superficialis, considered primitive, is found. It contains most American elapids (*Micrurus*), *Calliophis*, African elapid genera (except *Dendroaspis*), *Naja* and most sea snakes and the following Australasian forms: *Glyphodon*, *Furina*, *Cacophis*, *Vermicella**, *Neelaps**, *Simoselaps**, *Apistocalamus*, *Toxicocalamus*, *Ultrocalamus*, *Ogmodon*, *Loveridgelaps*, *Elapognathus*, *Drysdalia**, *Cryptophis**, and *Pseudonaja**.

—In Group 2, with the "Oxyuranus type" of adductor externus superficialis, the following are included: *Denisonia maculata*, *D. devisii*, *Acanthophis*,

Hoplocephalus, *Salomonelaps*, *Drysdalia coronata*, *Notechis*, *Tropidechis*, *Oxyuranus*, and *Echiopsis**.

—In Group 3, the "Pseudechis type" of adductor externus superficialis occurs. The group is almost confined to Australasian terrestrial elapids but includes also *Astrotia*, *Laticauda* and *Parapistocalamus*. Others are *Pseudechis*, *Micropechis*, *Unechis gouldi**, *U. nigrostriatus*, *U. carpentariae*, *U. flagellum*, *Suta*, *Austrelaps* and *Denisonia punctata*.

—Group 4 has the "Demansia type" of adductor externus superficialis, most easily derived from the "Pseudechis type". This group contains the sea snakes *Laticauda schistorhynchus* and *Hydrophis* (*Parahydrophis*) *mertoni* as well as *Rhinoplocephalus*, *Hemiaspis**, *Demansia* and *Aspidomorphus*.

In a subsequent analysis of Australasian elapids, McDowell (1970) defined two groups of genera: (1) the "Vermicella group" consisting of *Vermicella* (sensu McDowell 1967, see above, Section 2[d]) within Australia, *Salomonelaps*, and *Loveridgelaps* within the Solomon Islands and *Ogmodon* in Fiji; and (2) the "Pseudechis group" including *Micropechis* in New Guinea, *Pseudechis*, *Austrelaps* (for *A. superbus* only), *Suta* (for *Suta*, *Parasuta* and *Unechis* of Worrell, 1963) as well as *Denisonia fasciata*, *D. punctata* and "Cryptophis" (*Unechis*) *flagellum*. These species groups and the ones described above (McDowell, 1967) were apparently elevated to tribal status in the classification of Smith *et al.* (1977). These generic relationships or tribal affinities based on the morphological data represent the first groupings tested by biochemical means.

3. The Biochemical Data

In addition to the classifications based on morphological criteria, the possible relationships indicated by venom characterization and immunological studies are of interest. Unfortunately, data are generally available only for the species of larger Australian elapids owing to the difficulty in obtaining venom and blood samples from the smaller varieties. Minton & da Costa (1975) indicated close affinities between sea snakes and the two Australian terrestrial elapids *Denisonia* (= *Austrelaps*) *superba* and *Notechis* when their venoms were cross-reacted to other venoms. They also pointed out that *Notechis* venom did not react with *Denisonia* (*Austrelaps*) antiserum though these gross measures were intended to determine the relationship of these terrestrial elapids to sea snakes and not the intergeneric relationships of the Australian forms. In a more recent study, Minton (1981) analysed serological data from 11 genera native to eastern New South Wales and found *Pseudechis*, *Pseudonaja* and *Tropidechis* to be closely related while *Acanthophis*, *Demansia*, *Hemiaspis* and *Vermicella* were somewhat remote from this group. No comment was made on the interrelationships of the latter three genera. Coulter *et al.* (1981) examined the venoms of *Pseudechis*, *Pseudonaja*, *Austrelaps*, *Acanthophis*, *Oxyuranus* and *Notechis*, as well as Asian

terrestrial elapids and the sea snake *Enhydrina*, by enzyme immunoassay (EIA) and agreed with Minton & da Costa (1975) that the venoms of sea snakes were closely related to those of Australian elapids but not to those of the Asiatic species. The venoms of several Australian species differed greatly in respect to each other and it is interesting to note that in the reaction of species to anti-Notexin (from *Notechis*), as assayed by EIA, *Austrelaps* gave a reaction most similar to *Notechis* itself. Morrison (pers. comm.) has found great similarities in the venom characteristics of *Tropidechis* and *Notechis* with an immunological cross-reactivity of greater than 50%. The venom studies of both Saint Girons & Detrait (1980) and Fohlman (1979) point to a close similarity of the venoms of *Oxyuranus* and "*Parademansia*" (now = *Oxyuranus*) and their distinctness from *Pseudonaja*. Saint Girons & Detrait (1980) went on to demonstrate that the venoms of *Austrelaps* and *Pseudechis* possess many common antigens and they suggested that, along with *Bungarus*, *Austrelaps* and *Pseudechis* occupy "a central position among elapines of the Old World". They concluded that Australian genera do not form a homogeneous group, since the venoms of many species share antigens with *Bungarus*, whereas *Oxyuranus*, "*Parademansia*" (= *Oxyuranus*) and *Pseudonaja* have very weak cross-reactivity with other elapids.

It should be recalled from the previous section that the MC'F work of Cadle & Gorman demonstrated that *Demansia* was distinctive among Australian elapids in displaying the greatest immunological distance from all the elapid reference species they used and thus may be phylogenetically distinct.

From the limited chemotaxonomic data several inadequacies are evident. First, with the exception of the preliminary report of Minton (1981), none of the phylogenetic studies utilizing MC'F and immunodiffusion were initiated within Australia. The sample species studied were consequently very limited. As for the venom analysis, only one study, that of Saint Girons & Detrait (1980), appears to have been initiated to elucidate phylogenetic relationships and it, like those studies within Australia, was limited to species containing large specimens from which adequate venom samples are more commonly available.

4. A Summary of the Taxonomic Relationships of Australian Terrestrial Elapids

This review of morphological and chemotaxonomic characters, and the classifications derived from them, demonstrates that only two (*Rhinoplocephalus* and *Hoplocephalus*) of the 25 genera of Australian elapid snakes have not been altered taxonomically in the past two and a half decades. This reflects the small measure of agreement on intergeneric relationships, and indeed on the definition of suprageneric or tribal affinities.

Looking at the generic allocation of species, genera *Acanthophis*, *Demansia*, *Hoplocephalus*, *Oxyuranus*, *Pseudechis* and *Pseudonaja* appear clearly defined

though there are species within most of these that are obviously composite. However, many species that made up Boulenger's *Denisonia* continue to be problematic. In practice there remain two schools of thought. That following Storr (1964, 1981b) would treat *Denisonia* as a large genus in similar fashion to Boulenger (1896), though recognizing species group relationships within the genus. It should be recalled, however, that Storr (1982) has transferred the species of Worrell's *Drysdalia* from *Denisonia* to *Notechis* along with *Elapognathus*, *Austrelaps* and *Brachyaspis* (= *Echiopsis*).

An alternative school of thought has been expressed through the works of Cogger (1975b, 1979), where the generic groupings of the species formerly allocated to *Denisonia* and other complexes generally rely on the morphological data of McDowell, though the generic designations do not (see Cogger *et al.*, 1983). These efforts to express species relationships highlight the lack of agreement on the definition of generic and tribal categories. Though this may be a matter of semantics it is surely essential that an understanding precede efforts to express intergeneric relationships.

These areas of nomenclatural controversy point out those groups for which additional analyses must be performed before relationships are understood and a consensus met. Both ecological and morphological data have suggested a dichotomy between *D. devisii* and *D. maculata* on the one hand and *D. fasciata* and *D. punctata* on the other. Additionally, the genus *Unechis* (*sensu* Cogger, 1975) may be composite with some species showing affinities to *Suta* and *D. punctata* while others resemble *Cryptophis pallidiceps*. The ecological data of Shine have divided *Simoselaps* and *Neelaps* into distinct groupings while demonstrating similarities between *Tropidechis* and *Notechis*. These associations along with the relationships of the species making up *Furina* and *Glyphodon* are clearly the areas of most fruitful investigation.

5. Concluding Remarks

The data reviewed here and the resulting variety of classifications demonstrate that the morphological data reported thus far have failed to resolve the taxonomic questions. The biochemical data offer new hope in that they provide a novel data base that in some vertebrate groups has been found to be a powerful taxonomic tool. Such studies are, however, lacking in that they have been limited to small sample sizes of species of the larger elapids. To be effective there must be a cooperative effort to provide workers with live material from a broad representation of species. Only through a synthesis of more complete morphological, biochemical and cytological data sets will a meaningful and stable taxonomy be derived.

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Table 1. Genera of Proteroglyphs

This table lists all genera of proteroglyph snakes and where available their common names and relevant comments from the literature. An attempt has been made to list genera according to current tribal designations (see Smith *et al.*, 1977, and Harding & Welch, 1980). Unfortunately, none of the published classifications derived from the morphological studies of McDowell have specified the genera included in these tribes.

Family ELAPIDAE (Palatine Erectors)**Subfamily BUNGARINAE****Tribe Bungarini**

<i>Bungarus</i> Daudin, 1803 (12 spp.)	Kraits; India, SE Asia, Malaysia, Indonesia	Primitive among proteroglyphs (McDowell, 1970)
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Tribe Najini

<i>Aspidelaps</i> Fitzinger, 1843 (2 spp.)	Shield-nosed cobras; Africa	
<i>Boulengerina</i> Dollo, 1886 (2 spp.)	Water cobras; Africa	Primitive among proteroglyphs (McDowell, 1970)
<i>Dendroaspis</i> Schlegel, 1848 (4 spp.)	Mambas; Africa	Subfamily Dendroaspidinae (Romer, 1956)
<i>Elapsoidea</i> Bacage, 1866 (6 spp.)	African garter snakes	Primitive among proteroglyphs (McDowell, 1970)
<i>Hemachatus</i> Fleming, 1822 (1 sp.)	Ringhals Cobra, Africa	
<i>Naja</i> Laurenti, 1768 (6 spp.)	Cobras; Africa, Asia, India, Philippines, etc.	
<i>Ophiophagus</i> Günther, 1864 (1 sp.)	King Cobra; India, Asia, Indonesia, etc.	
<i>Paranaja</i> Loveridge, 1944 (1 sp.)	Burrowing Cobra; Africa	Primitive among proteroglyphs (McDowell, 1970)
<i>Pseudohaje</i> Günther, 1858 (2 spp.)	Tree cobras; Africa	
<i>Walterinnesia</i> Lataste, 1887 (1 sp.)	Desert Cobra	

Subfamily ELAPINAE**Tribe Elapini**

<i>Calliophis</i> Gray, 1834 (includes former <i>Hemibungarus</i> (10 spp.))	Asian coral snakes	} Micruridae of Duellman, 1979
<i>Leptomicrurus</i> Schmidt, 1937 (= <i>Micrurus</i>) (3 spp.)	Coral snakes	
<i>Micruroides</i> Schmidt, 1928 (1 sp.)	Arizona Coral Snake; U.S.A.	
<i>Micrurus</i> Wagler, 1824 (43 spp.)	Coral snakes; the Americas	

Tribe Maticorini

<i>Maticora</i> Gray, 1834 (2 spp.)	Coral snakes
<i>Parapistocalamus</i> Roux, 1934 (1 sp.)	Hediger's Snake; Bougainville I.

Tribe Laticaudini

<i>Laticauda</i> Laurenti, 1768 (5 spp.)	Sea kraits	Family Laticaudidae Burger and Natsumo, 1974
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Family HYDROPHIIDAE (Palatine Draggers)

Subfamily OXYURANINAE (Terrestrial palatine draggers)

<i>Acanthophis</i> Daudin, 1803 (2 spp.)	Death adders; Australia, Papua New Guinea and islands.
<i>Aspidomorphus</i> Fitzinger, 1803 (2 spp.)	
<i>Austrelaps</i> Worrell, 1963 (1 sp.)	Copperhead; Australia
<i>Cacophis</i> Günther, 1863 (3 spp.)	Crowned snakes; Australia
<i>Cryptophis</i> Worrell, 1961 (2 spp.)	Small-eyed snakes; Australia
<i>Demansia</i> Gray, 1842 (5 spp.)	Whip snakes; Australia, Papua New Guinea
<i>Denisonia</i> Krefft, 1869 (4 spp.)	Australia
<i>Drysdalia</i> Worrell, 1961 (4 spp.)	White-lipped snakes; Australia
<i>Echiopsis</i> Fitzinger, 1843 (2 spp.)	Desert Snake; Australia
<i>Elapognathus</i> Boulenger, 1869 (1 sp.)	Little Brown Snake; Australia
<i>Furina</i> Duméril, Bibron and Duméril, 1854 (1 sp.?)	Red-naped Snake; Australia
<i>Glyphodon</i> Günther, 1858 (3 spp.)	Australia, Papua New Guinea
<i>Hemiaspis</i> Fitzinger, 1861 (2 spp.)	(<i>Drepanodontis</i>) Marsh Snake; Australia
<i>Hoplocephalus</i> Cuvier, 1832 (3 spp.)	Broad-headed snakes; Australia
<i>Loveridgelaps</i> McDowell, 1970 (1 sp.)	Banded Small-eyed Snake; Solomon Is.
<i>Micropechis</i> Boulenger, 1896 (1 sp.)	New Guinea Small-eyed Snake; Papua New Guinea
<i>Neelaps</i> Günther, 1863 (2 spp.)	Australia
<i>Notechis</i> Boulenger, 1896 (2 spp.)	Tiger snakes; Australia
<i>Ogmodon</i> Peters, 1864 (1 sp.)	Fiji
<i>Oxyuranus</i> Kinghorn, 1923 (2 spp.)	Taipans; Australia, Papua New Guinea
<i>Pseudechis</i> Wagler, 1830 (5 spp.)	Black snakes and King Brown; Australia, Papua New Guinea
<i>Pseudonaja</i> Günther, 1858 (6 spp.)	Brown snakes; Australia, Papua New Guinea
<i>Rhinoplocephalus</i> Muller, 1885 (1 sp.)	Muller's Snake, Australia
<i>Salomonelaps</i> McDowell, 1970 (1 sp.)	Solomon Islands

Subfamily Acanthophinae Dowling & Duellman, 1978

Presumed tribe Acanthophini

"*Demansia* Group", related to *Demansia*, *Hemiaspis*, *Rhinoplocephalus* (McDowell, 1967)

"*Pseudechis*" group of McDowell, 1970

Presumed tribe Glyphodontini, related (very close) to *Aspidomorphus* (McDowell, 1967)

"*Demansia* Group", related to *Aspidomorphus*, *Rhinoplocephalus* and *Hemiaspis*

"*Pseudechis* Group" (*D. fasciata* and *D. punctata*)

D. coronata, *Oxyuranus* type of adductor externus superficialis

Presumed tribe Glyphodontini (Smith, 1977; McDowell, 1967)

Presumed tribe Glyphodontini (Smith, 1977; McDowell, 1967)

"*Demansia* Group", related to *Demansia*, *Rhinoplocephalus*, *Aspidomorphus* (McDowell, 1967)

Maybe Oxyuranini; *Oxyuranus* type of adductor externus superficialis

"*Vermicella* Group"

"*Pseudechis* Group"

Presumed tribe Apistocalamini (Smith *et al.*, 1977; McDowell, 1969)

Oxyuranus type of adductor externus superficialis

"*Vermicella* Group": most primitive palatine dragger (McDowell, 1970)

Presumed tribe Oxyuranini

"*Pseudechis* Group" of McDowell, 1970

Presumed tribe Pseudonajini

"*Demansia* Group", related to *Demansia*, *Aspidomorphus*, *Hemiaspis* (McDowell, 1967)

"*Vermicella* Group" of McDowell, 1970

<i>Simoselaps</i> Jan, 1859 (6+ spp.)	Desert banded snakes; Australia	Presumed tribe Apistocalamini (Smith, 1977; McDowell, 1969)
<i>Suta</i> Worrell, 1961 (1 sp.)	Curl snakes; Australia	" <i>Pseudechis</i> Group" of McDowell, 1970
<i>Toxicocalamus</i> Boulenger, 1896 (9 spp.) (includes <i>Apistocalamus</i> and <i>Ultracalamus</i>)	Papua New Guinea	Presumed tribe Apistocalamini (Smith, 1977; McDowell, 1969)
<i>Tropidechis</i> Günther, 1863 (1 sp.)	Rough-scaled snake; Australia	Maybe Oxyuranini; " <i>Oxyuranus</i> type" of adductor externus superficialis
<i>Unechis</i> Worrell, 1961 (7+ spp.)	Blackheaded snakes; Australia	" <i>Pseudechis</i> Group" of McDowell, 1970
<i>Vermicella</i> Günther, 1858 (2 spp.)	Bandy-bandy, Australia	" <i>Vermicella</i> Group" of McDowell, 1970
Subfamily HYDROPHIINAE	True sea snakes	Family Hydrophiidae of Burger and Natsuno, 1974
Tribe Ephalophiini		Subfamily Ephalophiinae of Burger and Natsuno, 1974
<i>Ephalophis</i> Smith, 1931 (1 sp.) (for <i>E. greyi</i> only)		Primitive in many respects, shows relationship to terrestrial elapids <i>Rhinoplocephalus</i> , <i>Hemiaspis</i> (McDowell, 1969, 1974)
<i>Parahydrophis</i> Burger and Natsuno, 1974 (1 sp.)		Related to <i>Ephalophis</i> but stands at the base of lineages leading to both Aipysurini and Hydrophiini (McDowell, 1969)
Tribe Hydrelapini		" <i>Hydrelaps</i> Group" of McDowell, 1969
<i>Hydrelaps</i> Boulenger, 1896 (1 sp.)		In subfamily Ephalophinae of Burger and Natsuno, 1974
Tribe Aipysurini		In subfamily Ephalophinae of Burger and Natsuno, 1974
<i>Aipysurus</i> Lacépède, 1804 (7 spp.)		" <i>Aipysurus</i> Group" of McDowell, 1969
<i>Emydocephalus</i> Krefft, 1869 (2 spp.)		" <i>Aipysurus</i> Group" of McDowell, 1969
Tribe Hydrophiini		All below in subfamily Hydrophiinae of Burger and Natsuno, 1974
<i>Acalyptophis</i> Boulenger, 1896 (1 sp.)		
<i>Astrotia</i> Fisher, 1856 (1 sp.)		
<i>Disteira</i> Lacépède, 1804 (2 spp.) (contains some <i>Hydrophis</i> and <i>Hydrus</i>)		Considered a subgenus by Burger and Natsuno (1974); McDowell (1972) recognizes 5 species.
<i>Enhydrina</i> Gray, 1849 (1 sp.)		
<i>Hydrophis</i> Latreille, 1802 (24 spp.) (contains <i>Aturia</i>)		
<i>Kerilia</i> Gray, 1849 (1 sp.)		
<i>Kolpophis</i> Smith, 1926 (1 sp.)		
<i>Lapemis</i> Gray, 1835 (2 spp.)		Includes <i>Kolpophis</i> and <i>praescutata</i> —McDowell, 1972
<i>Thalassophis</i> Schmidt, 1852 (2 spp.)		Included in <i>Lapemis</i> by Burger and Natsuno, 1974
<i>Pelamis</i> Daudin, 1803 (1 sp.)	Pelagic sea snake	

Table 2. Nomenclatural History

This table provides a comparison of all major classifications of Australian terrestrial elapids from Günther (1858) to the present. Accompanying the table is an alphabetical list of currently recognized species cross-referenced to the classification of Cogger (1975b, 1979) in the far left hand column. Species recognized since Cogger (1979) are marked with an asterisk (*). Blank spaces in the table indicate that the particular worker

Cogger 1975b, 1979	Storr 1982, 1981a,b,c, 1979, 1967	McDowell 1967,1970, 1969	Worrell 1961, 1963,a,b 1950, 1960
1.1 <i>Acanthophis antarcticus</i>	<i>Acanthophis</i>	<i>Acanthophis</i>	<i>Acanthophis</i>
1.2 <i>A. pyrrhus</i>	<i>Acanthophis</i>		<i>Acanthophis</i>
	1.3 * <i>A. praelongus</i>		
2. <i>Austrelaps superbus</i>	<i>Notechis</i>	<i>Austrelaps</i>	<i>Austrelaps</i>
3.1 <i>Cacophis harriettae</i>		<i>Cacophis</i>	<i>Glyphodon</i>
3.2 <i>C. krefftii</i>		<i>Cacophis</i>	<i>Cacophis</i>
3.3 <i>C. squamulosus</i>		<i>Cacophis</i>	<i>Aspidomorphus</i>
4.1 <i>Cryptophis nigrescens</i>	<i>Denisonia</i>	" <i>Denisonia</i> "	<i>Cryptophis</i>
4.2 <i>C. pallidiceps</i>	<i>Denisonia</i>	" <i>Denisonia</i> "	<i>Cryptophis</i>
5.1 <i>Demansia atra</i>	<i>Demansia</i>		
5.2 <i>D. olivacea</i>	<i>Demansia</i>	<i>Demansia</i>	<i>Demansia</i>
5.3 <i>D. psammophis</i>	<i>Demansia</i>	<i>Demansia</i>	<i>Demansia</i>
5.4 <i>D. torquata</i>		<i>Demansia</i>	<i>Demansia</i>
	5.6 * <i>D. simplex</i>		
	5.7 * <i>D. reticulata</i>		
	5.8 * <i>D. papuensis</i>		
6.1 <i>Denisonia devisii</i>	<i>Denisonia</i>	<i>Denisonia</i>	<i>Denisonia</i>
6.2 <i>D. fasciata</i>	<i>Denisonia</i>	<i>Suta</i>	<i>Denisonia</i>
6.3 <i>D. maculata</i>	<i>Denisonia</i>	<i>Denisonia</i>	<i>Denisonia</i>
6.4 <i>D. punctata</i>	<i>Denisonia</i>	<i>Suta</i>	<i>Denisonia</i>
7.1 <i>Drysdalia coronata</i>	<i>Notechis</i>	" <i>Denisonia</i> "	<i>Drysdalia</i>
7.2 <i>D. coronoides</i>	<i>Notechis</i>		<i>Drysdalia</i>
7.3 <i>D. mastersi</i>	<i>Notechis</i>		<i>Drysdalia</i>
7.4 <i>D. rhodogaster</i>	<i>Notechis</i>		
8.1 <i>Echiopsis curta</i>	<i>Brachyaspis</i>	<i>Brachyaspis</i>	<i>Brachyaspis</i>
8.2 * <i>E. atriceps</i>	<i>Brachyaspis</i>		
9. <i>Elapognathus minor</i>	<i>Notechis</i>	<i>Elapognathus</i>	<i>Elapognathus</i>
10. <i>Furina diadema</i>	<i>Furina</i>	<i>Furina</i>	<i>Brachysoma</i>
	10.2 * <i>F. ornata</i> (= <i>christieanus</i>)		<i>Lunelaps</i>
11.1 <i>Glyphodon barnardi</i>	<i>Furina</i>		<i>Lunelaps</i>
11.2 <i>G. dunmalli</i>			<i>Glyphodon</i>
11.3 <i>G. tristis</i>	<i>Furina</i>	<i>Glyphodon</i>	<i>Glyphodon</i>
12.1 <i>Hemiaspis damelii</i>	<i>Denisonia</i>	<i>Drepanodontis</i>	<i>Drepanodontis</i>
12.2 <i>H. signata</i>	<i>Denisonia</i>	<i>Drepanodontis</i>	<i>Austrelaps</i>
13.1 <i>Hoplocephalus bitorquatus</i>		<i>Hoplocephalus</i>	<i>Hoplocephalus</i>
13.2 <i>H. bungaroides</i>		<i>Hoplocephalus</i>	<i>Hoplocephalus</i>
13.3 <i>H. stephensi</i>		<i>Hoplocephalus</i>	<i>Hoplocephalus</i>
14.1 <i>Neelaps bimaculatus</i>	<i>Vermicella</i>	<i>Rhynchoelaps</i>	<i>Narophis</i>
14.2 <i>N. calonotus</i>	<i>Vermicella</i>	<i>Rhynchoelaps</i>	<i>Melwardia</i>
15.1 <i>Notechis ater</i>	<i>Notechis</i>		<i>Notechis</i>
15.2 <i>N. scutatus</i>	<i>Notechis</i>	<i>Notechis</i>	<i>Notechis</i>
16. <i>Oxyuranus scutellatus</i>		<i>Oxyuranus</i>	<i>Oxyuranus</i>
17. <i>Parademansia (O.) microlepidota</i>			<i>Oxyuranus</i>
18.1 <i>Pseudechis australis</i>	<i>Pseudechis</i>	<i>Pseudechis</i>	<i>Pseudechis</i>
18.2 <i>P. colletti</i>	<i>Pseudechis</i>	<i>Pseudechis</i>	<i>Pseudechis</i>
18.3 <i>P. guttatus</i>	<i>Pseudechis</i>		<i>Pseudechis</i>
18.4 <i>P. porphyriacus</i>	<i>Pseudechis</i>	<i>Pseudechis</i>	<i>Pseudechis</i>
	18.5 * <i>P. butleri</i> (Smith)		

of Australian Terrestrial Elapids

made no reference to the species. By utilizing the list of synonyms in Table 3 coupled with this table the reader can determine the currently recognized species name as well as examine its taxonomic stability through time and that of its congeners. It should be realized that the classifications of both Cogger and Storr are currently in use.

Kinghorn 1956	Loveridge 1934	Krefft 1869	Boulenger 1896	Günther 1858
<i>Acanthophis</i> <i>Acanthophis</i>	<i>Acanthophis</i> <i>Acanthophis</i>	<i>Acanthophis</i>	<i>Acanthophis</i>	
<i>Denisonia</i> <i>Aspidomorphus</i> <i>Aspidomorphus</i> <i>Aspidomorphus</i> <i>Denisonia</i> <i>Denisonia</i>	<i>Denisonia</i> <i>Pseudelaps</i> <i>Pseudelaps</i> <i>Denisonia</i> <i>Denisonia</i>	<i>Hoplocephalus</i> <i>Cacophis</i> <i>Cacophis</i> <i>Petrodymon</i> <i>Hoplocephalus</i>	<i>Denisonia</i> <i>Pseudelaps</i> <i>Pseudelaps</i> <i>Pseudelaps</i> <i>Denisonia</i> <i>Denisonia</i> <i>Diemenia</i>	<i>Hoplocephalus</i> <i>Hoplocephalus</i>
<i>Demansia</i> <i>Demansia</i> <i>Demansia</i>	<i>Demansia</i> <i>Demansia</i>	<i>Diemenia</i> <i>Diemenia</i> <i>Diemenia</i>	<i>Diemenia</i> <i>Diemenia</i> <i>Diemenia</i>	 <i>Demansia</i> <i>Demansia</i>
<i>Demansia</i>	<i>Demansia</i>	<i>Diemenia</i>		<i>Demansia</i>
<i>Denisonia</i> <i>Denisonia</i> <i>Denisonia</i> <i>Denisonia</i> <i>Denisonia</i> <i>Denisonia</i> <i>Denisonia</i>	 <i>Denisonia</i> <i>Denisonia</i> <i>Denisonia</i> <i>Denisonia</i>	 <i>Denisonia</i> <i>Hoplocephalus</i> <i>Hoplocephalus</i> <i>Hoplocephalus</i>	 <i>Denisonia</i> <i>Denisonia</i> <i>Denisonia</i> <i>Denisonia</i> <i>Pseudelaps</i> <i>Denisonia</i>	 <i>Hoplocephalus</i> <i>Hoplocephalus</i>
<i>Denisonia</i>		<i>Hoplocephalus</i>	<i>Brachyaspis</i>	<i>Hoplocephalus</i>
<i>Elapognathus</i> <i>Aspidomorphus</i> <i>Aspidomorphus</i>	 <i>Pseudelaps</i> <i>Pseudelaps</i>	<i>Hoplocephalus</i> <i>Cacophis</i>	<i>Elapognathus</i> <i>Pseudelaps</i> <i>Pseudelaps</i>	<i>Hoplocephalus</i> <i>Brachysoma</i> <i>Glyphodon</i>
<i>Glyphodon</i>				
<i>Glyphodon</i> <i>Denisonia</i> <i>Denisonia</i> <i>Hoplocephalus</i> <i>Hoplocephalus</i> <i>Hoplocephalus</i> <i>Vermicella</i> <i>Vermicella</i> <i>Notechis</i> <i>Notechis</i> <i>Oxyuranus</i> <i>Parademansia</i> <i>Pseudechis</i> <i>Pseudechis</i> <i>Pseudechis</i> <i>Pseudechis</i>	 <i>Denisonia</i> <i>Hoplocephalus</i> <i>Hoplocephalus</i> <i>Furina</i> <i>Notechis</i>	 <i>Brachysoma</i> <i>Hoplocephalus</i> <i>Hoplocephalus</i> <i>Hoplocephalus</i> <i>Hoplocephalus</i> <i>Furina</i> <i>Brachysoma</i> <i>Hoplocephalus</i> <i>Hoplocephalus</i> <i>Pseudechis</i> <i>Pseudechis</i>	 <i>Glyphodon</i> <i>Denisonia</i> <i>Denisonia</i> <i>Hoplocephalus</i> <i>Hoplocephalus</i> <i>Hoplocephalus</i> <i>Furina</i> <i>Furina</i> <i>Notechis</i> <i>Notechis</i> <i>Pseudechis</i> <i>Pseudechis</i> <i>Pseudechis</i>	 <i>Glyphodon</i> <i>Hoplocephalus</i> <i>Brachysoma</i> <i>Brachysoma</i> <i>Pseudechis</i>

Cogger 1975b, 1979	Storr 1982, 1981a,b,c, 1979, 1967	McDowell 1967, 1970, 1969	Worrell 1961, 1963,a,b 1950, 1960
19.1 <i>Pseudonaja affinis</i>	<i>Pseudonaja</i>		<i>Pseudonaja</i>
19.2 <i>P. guttata</i>	<i>Pseudonaja</i>	"Demansia"	<i>Pseudonaja</i>
19.3 <i>P. ingrami</i>	<i>Pseudonaja</i>		<i>Pseudonaja</i>
19.4 <i>P. modesta</i>	<i>Pseudonaja</i>	"Demansia"	<i>Pseudonaja</i>
19.5 <i>P. nuchalis</i>	<i>Pseudonaja</i>	"Demansia"	<i>Pseudonaja</i>
19.6 <i>P. textilis</i>	<i>Pseudonaja</i>	"Demansia"	<i>Pseudonaja</i>
20. <i>Rhinoplocephalus bicolor</i>	<i>Rhinoplocephalus</i>	<i>Rhinoplocephalus</i>	<i>Rhinoplocephalus</i>
21.1 <i>Simoselaps australis</i>	<i>Vermicella</i>	<i>Rhynchoelaps</i>	<i>Brachyurops</i>
	21.2 * <i>V. anomalus</i>		
	21.3 * <i>V. approximans</i>		<i>Rhinelaps</i>
21.4 <i>S. bertholdi</i>	<i>Vermicella</i>	<i>Rhynchoelaps</i>	<i>Rhynchoelaps</i>
21.5 <i>S. fasciolatus</i>	<i>Vermicella</i>	<i>Rhynchoelaps</i>	<i>Rhinelaps</i>
21.6 <i>S. incinctus</i>	<i>Vermicella</i>	<i>Rhynchoelaps</i>	<i>Rhynchoelaps</i>
21.7 <i>S. semifasciatus</i>	<i>Vermicella</i>	<i>Rhynchoelaps</i>	<i>Brachyurops</i>
	21.8 * <i>V. littoralis</i>		
21.9 <i>S. warro</i>	<i>Furina</i>	<i>Rhynchoelaps</i>	<i>Rhinelaps</i>
21.10 <i>S. minimus</i>	<i>Vermicella</i>		<i>Melwardia</i>
22. <i>Suta suta</i>	<i>Denisonia</i>	<i>Suta</i>	<i>Suta</i>
23. <i>Tropidechis carinatus</i>		<i>Tropidechis</i>	<i>Tropidechis</i>
24.1 <i>Unechis brevicaudus</i>	= * <i>D. nigriceps</i>	<i>Suta</i>	<i>Parasuta</i>
24.2 <i>U. carpentariae</i> (= <i>boschmai</i>)	<i>Denisonia</i>	<i>Suta</i>	<i>Unechis</i>
24.3 <i>U. flagellum</i>	<i>Denisonia</i>	<i>Suta</i>	<i>Cryptophis</i>
24.4 <i>U. gouldii</i>	<i>Denisonia</i>	<i>Suta</i>	<i>Parasuta</i>
	<i>Denisonia</i>	<i>Suta</i>	24.4.1 <i>Denisonia d'ever</i>
24.5 <i>U. monachus</i>	<i>Denisonia</i>		
24.6 <i>U. nigrostriatus</i>		<i>Suta</i>	<i>Parasuta</i>
	24.7 * <i>D. spectabilis</i>		
25.1 <i>Vermicella annulata</i>	<i>Vermicella</i>	<i>Vermicella</i>	<i>Vermicella</i>
25.2 <i>V. multifasciata</i>			

Currently Recognized Species of Australian Elapids (derived largely from the checklist currently in press by Cogger *et al.*, 1983)

<i>affinis</i> , P., Günther, 1872	19.1	<i>bungaroides</i> , H., (Schlegel, 1837)	13.2
<i>annulata</i> , V., (Gray, 1841)	25.1	<i>butleri</i> , P., Smith, 1981	18.5
<i>anomalus</i> , S., (Sternfield, 1919)	21.2	<i>calonotus</i> , N., (Duméril, Bibron & Duméril, 1854)	14.2
<i>antarcticus</i> , A., (Shaw & Nodder, 1802)	1.1	<i>carinatus</i> , T., (Krefft, 1863)	23.0
<i>approximans</i> , S., (Glauert, 1954)	21.3	<i>carpentariae</i> , U., (= <i>boschmai</i>)	24.2
<i>ater</i> , N., (Krefft, 1856)	15.1	<i>colletti</i> , P., Boulenger, 1902	18.2
<i>atra</i> , D., (Macleay, 1884)	5.1	<i>coronata</i> , D., (Schlegel, 1837)	7.1
<i>atriceps</i> , E., (Storr, 1980)	8.0	<i>coronoides</i> , D., (Günther, 1858)	7.2
<i>australis</i> , P., (Gray, 1842)	18.0	<i>curta</i> , E., (Schlegel, 1837)	8.0
<i>australis</i> , S., (Krefft, 1864)	21.1	<i>damelii</i> , H., (Günther, 1876)	12.0
<i>barnardi</i> , G., Kinghorn, 1939	11.0	<i>devisii</i> , D., Waite & Longman, 1920	6.1
<i>bertholdi</i> , S., (Jan, 1859)	21.4	<i>diadema</i> , F., (Schlegel, 1837)	10.0
<i>bicolor</i> , R., Müller, 1885	20.0	<i>dunmalli</i> , G., Worrell, 1955	11.2
<i>bimaculatus</i> , N., (Duméril, Bibron & Duméril, 1854)	14.0	<i>dwyeri</i> , U., (Worrell, 1963)	24.4.1
<i>bitorquatus</i> , H., (Jan, 1859)	13.0	<i>fasciata</i> , D., Rosén, 1905	6.2
<i>boschmai</i> , U., (Brongersma & Knapp-Van Meeuwen, 1961)	24.2	<i>fasciolatus</i> , S., (Günther, 1872)	21.5
		<i>flagellum</i> , U., (McCoy, 1878)	24.3
		<i>gouldii</i> , U., (Gray, 1841)	24.4.2
		<i>guttata</i> , P., (Parker, 1926)	19.2
		<i>guttatus</i> , P., DeVis, 1905	18.3

Ginghorn 1956	Loveridge 1934	Krefft 1869	Boulenger 1896	Günther 1858
<i>Demansia</i>	<i>Demansia</i>			
<i>Demansia</i>				
<i>Demansia</i>				
<i>Demansia</i>	<i>Demansia</i>		<i>Diemenia</i>	<i>Cacophis</i>
<i>Demansia</i>	<i>Demansia</i>	<i>Pseudonaja</i>	<i>Diemenia</i>	<i>Pseudonaja</i>
<i>Demansia</i>	<i>Demansia</i>	<i>Diemenia</i>	<i>Diemenia</i>	
<i>Rhinoplocephalus</i>			<i>Rhinoplocephalus</i>	
<i>Brachyurops</i>	<i>Rhynchoelaps</i>	<i>Brachyurops</i>	<i>Rhynchoelaps</i>	
<i>Rhinelaps</i>				
<i>Rhynchoelaps</i>	<i>Rhynchoelaps</i>		<i>Rhynchoelaps</i>	
<i>Rhinelaps</i>			<i>Rhynchoelaps</i>	
<i>Brachyurops</i>			<i>Rhynchoelaps</i>	
<i>Rhinelaps</i>				
<i>Denisonia</i>	<i>Denisonia</i>		<i>Denisonia</i>	
<i>Tropidechis</i>		<i>Tropidechis</i>	<i>Tropidechis</i>	
<i>Denisonia</i>	<i>Denisonia</i>		<i>Denisonia</i>	
<i>Denisonia</i>	<i>Denisonia</i>		<i>Denisonia</i>	
<i>Denisonia</i>	<i>Denisonia</i>		<i>Denisonia</i>	<i>Hoplocephalus</i>
<i>Denisonia</i>			<i>Denisonia</i>	
<i>Vermicella</i>	<i>Furina</i>	<i>Vermicella</i>	<i>Furina</i>	<i>Vermicella</i>

<i>harrietae</i> , C., Krefft, 1869	3.1	<i>porphyriacus</i> , P., (Shaw, 1794)	18.4
<i>incinctus</i> , S., (Storr 1968)	21.6	<i>praelongus</i> , A., Ramsay, 1877	1.3
<i>ingrami</i> , P., (Boulenger 1908)	19.3	<i>psammophis</i> , D., (Schlegel, 1837)	5.3
<i>krefftii</i> , C., Günther, 1863	3.2	<i>punctata</i> , D., Boulenger, 1896	6.4
<i>littoralis</i> , S., (Storr, 1968)	21.8	<i>pyrrhus</i> , A., Boulenger, 1898	1.2
<i>maculata</i> , D., (Steindachner, 1867)	6.3	<i>rhodogaster</i> , D., (Jan & Sordelli, 1873)	7.4
<i>mastersi</i> , D., (Krefft, 1866)	7.3	<i>scutatus</i> , N., (Peters, 1861)	15.2
<i>microlepidota</i> , O., (McCoy, 1879)	17.0	<i>scutellatus</i> , O., (Peters, 1867)	16.0
<i>minor</i> , E., (Günther, 1863)	9.0	<i>semifasciatus</i> , S., (Günther, 1863)	21.7
<i>minimus</i> , E., (Worrell, 1960)	21.10	<i>signata</i> , H., (Jan, 1859)	12.2
<i>modesta</i> , P., (Günther, 1872)	19.4	<i>simplex</i> , D., Storr, 1978	5.6
<i>monachus</i> , U., (Storr, 1964)	24.5	<i>spectabilis</i> , U., (Krefft, 1869)	24.7
<i>multifasciata</i> , V., (Longman, 1915)	25.2	<i>squamulosus</i> , C., (Duméril, Bibron & Duméril, 1859)	3.3
<i>nigrescens</i> , C., (Günther, 1862)	4.1	<i>stephensi</i> , H., Krefft, 1869	13.3
<i>nigriceps</i> , U., (Günther, 1863)	24.0	<i>superbus</i> , A., (Günther, 1858)	2.0
<i>nigrostriatus</i> , U., (Krefft, 1864)	24.6	<i>suta</i> , S., (Peters, 1854)	22.0
<i>nuchalis</i> , P., Günther, 1858	19.5	<i>textilis</i> , P., (Duméril, Bibron & Duméril, 1863)	19.6
<i>olivacea</i> , D., (Gray, 1842)	5.2	<i>torquata</i> , D., (Günther, 1862)	5.4
<i>ornata</i> , F., (Gray, 1842)	10.2	<i>tristis</i> , G., Günther, 1858	11.3
<i>pallidiceps</i> , C., (Günther, 1858)	4.2	<i>warro</i> , S., (DeVis, 1884)	21.9
<i>papuensis</i> , D., (Macleay, 1877)	5.8		

Table 3. Names applied to Australian snakes.

This table is a complete alphabetical list of all junior synonyms under which Australian proteroglyphs have been described and their authors. This information has been derived largely from the checklist currently in press by Cogger *et al.*, but differs from it in a few instances. The terrestrial and marine forms have been separated for the reader's convenience.

Terrestrial Proteroglyphs

<i>acanthophis</i> , <i>Ophryas</i> , Merrem, 1820	= <i>Acanthophis antarcticus</i>	<i>bertholdi</i> , <i>Elaps</i> , Jan, 1858	= <i>Simoselaps bertholdi</i>
<i>Acanthophis</i> Daudin, 1803	= <i>Acanthophis</i>	<i>bicolor</i> , <i>Rhinoplocephalus</i> , Müller, 1885	= <i>Rhinoplocephalus bicolor</i>
<i>Acanthophis</i> Berthold, 1827	= <i>Acanthophis</i>	<i>bicucullata</i> , <i>Furina</i> , McCoy, 1879	= <i>Pseudonaja textilis</i>
<i>aculeata</i> , <i>Boa</i> , Boulenger, 1896	= <i>Acanthophis antarcticus</i>	<i>bilineata</i> , <i>Furina</i> Duméril, Bibron & Duméril, 1854	= incertae sedis
<i>acutirostris</i> , <i>Demansia</i> , Mitchell, 1951	= <i>Pseudonaja nuchalis</i>	<i>bimaculata</i> , <i>Furina</i> , Duméril, 1854	= <i>Neelaps bimaculatus</i>
<i>affinis</i> , <i>Pseudonaja</i> , Günther, 1872	= <i>Pseudonaja affinis</i>	<i>bitorquata</i> , <i>Alecto</i> , Jan, 1859	= <i>Hoplocephalus bitorquatus</i>
<i>albiceps</i> , <i>Pseudelaps</i> , Boulenger, 1898	= <i>Simoselaps warro</i>	<i>blackmanii</i> , <i>Cacophis</i> , Krefft, 1869	= <i>Furina diadema</i>
<i>Alecto</i> Wagler, 1830	= <i>Pseudechis</i>	<i>boschmai</i> , <i>Denisonia</i> , Brongersma & Knaap- van Meeuwen, 1961	= <i>Unechis boschmai</i>
<i>ambigua</i> , <i>Boa</i> , Leach, 1814	= <i>Acanthophis antarcticus</i>	<i>Brachyaspis</i> Boulenger, 1896	= <i>Echiopsis</i>
<i>angulata</i> , <i>Denisonia</i> , DeVis, 1905	= <i>Hoplocephalus bitorquatus</i>	<i>Brachysoma</i> Fitzinger, 1843	= <i>Furina</i>
<i>angusticeps</i> , <i>Diemenia</i> , Macleay, 1888	= <i>Demansia olivacea</i>	<i>Brachyuropsis</i> Günther, 1863	= <i>Simoselaps</i>
<i>annulata</i> , <i>Calamaria</i> , Gray, 1841	= <i>Vermicella annulata</i>	<i>brankysi</i> , <i>Hoplocephalus</i> , Goldman, Hill & Stanbury, 1969	= <i>Austrelaps superbus</i>
<i>annulata</i> , <i>Demansia</i> , Günther, 1858	= <i>Pseudonaja textilis</i>	<i>bransbyi</i> , <i>Hoplocephalus</i> , Macleay, 1878	= <i>Austrelaps superbus</i>
<i>anomalus</i> , <i>Rhynchelaps</i> , Sternfield, 1919	= <i>Simoselaps anomalus</i>	<i>brevicauda</i> , <i>Denisonia</i> <i>nigrostriata</i> , Mitchell, 1951	= <i>Unechis nigriceps</i>
<i>antarctica</i> , <i>Boa</i> , Shaw & Nodder, 1802	= <i>Acanthophis antarcticus</i>	<i>brownii</i> , <i>Acanthophis</i> , Leach, 1814	= <i>Acanthophis antarcticus</i>
<i>approximans</i> , <i>Rhyncho-</i> <i>elaps</i> , Glauert, 1954	= <i>Simoselaps approximans</i>	<i>brunnea</i> , <i>Denisonia</i> , Mitchell, 1951	= <i>Pseudechis australis</i>
<i>aspidorhyncha</i> , <i>Diemenia</i> , McCoy, 1879	= <i>Pseudonaja nuchalis</i>	<i>bungaroides</i> , <i>Naja</i> , Schlegel, 1837	= <i>Hoplocephalus bungaroides</i>
<i>assimilis</i> , <i>Hoplocephalus</i> , Macleay, 1885	= <i>Cryptophis nigrescens</i>	<i>butleri</i> , <i>Pseudechis</i> , Smith, 1981	= <i>Pseudechis butleri</i>
<i>ater</i> , <i>Hoplocephalus</i> , Krefft, 1866	= <i>Notechis ater</i>	<i>Cacophis</i> Günther, 1863	= <i>Cacophis</i>
<i>atra</i> , <i>Diemenia</i> , Macleay, 1884	= <i>Demansia atra</i>	<i>caledonicus</i> , <i>Neelaps</i> , Hoffman, 1890	= <i>Neelaps calonotus</i>
<i>atriceps</i> , <i>Brachyaspis</i> , Storr, 1980	= <i>Echiopsis atriceps</i>	<i>calodera</i> , <i>Demansia</i> <i>olivacea</i> , Storr, 1978	= <i>Demansia olivacea</i>
<i>atropolios</i> , <i>Pseudoelaps</i> , Jan & Sordelli, 1873	= <i>Cacophis squamulosus</i>	<i>calonotos</i> , <i>Furina</i> , Duméril, 1853	= <i>Neelaps calonotus</i>
<i>australis</i> , <i>Naja</i> , Gray, 1842	= <i>Pseudechis australis</i>	<i>cambelli</i> , <i>Rhynchoelaps</i> , Kinghorn, 1929	= <i>Simoselaps semifasciatus</i>
<i>australis</i> , <i>Simotes</i> , Krefft, 1864	= <i>Simoselaps australis</i>	<i>canni</i> , <i>Oxyuranus</i> <i>scutellatus</i> , Slater, 1956	= <i>Oxyuranus scutellatus canni</i>
<i>australis</i> , <i>Tortrix</i> <i>Austrelaps</i> Worrell, 1963	= incertae sedis	<i>carinata</i> , <i>Diemenia</i> , Longman, 1915	= <i>Pseudonaja nuchalis</i>
<i>bancrofti</i> , <i>Denisonia</i> , DeVis, 1911	= <i>Furina diadema</i>	<i>carinatus</i> , <i>Hoplocephalus</i> Krefft, 1863	= <i>Tropidechis carinatus</i>
<i>bancrofti</i> , <i>Pseudelaps</i> , DeVis, 1911	= <i>Pseudonaja nuchalis</i>	<i>carpentariae</i> , <i>Hoploceph-</i> <i>alus</i> , Macleay, 1887	= <i>Suta suta</i>
<i>barnardi</i> , <i>Glyphodon</i> , Kinghorn, 1939	= <i>Glyphodon barnardi</i>		
<i>beckeri</i> , <i>Pseudoelaps</i> , Jan & Sordelli, 1873	= <i>Pseudonaja textilis</i>		

<i>carpentariae</i> , <i>Unechis</i> , Worrell, 1961	= <i>Unechis boschmai</i>	<i>Elapognathus</i> Boulenger, 1896	= <i>Elapognathus</i>
<i>cerastinus</i> , <i>Acanthophis</i> , Daudin, 1803	= <i>Acanthophis antarcticus</i>	<i>Euprepiosoma</i> Fitzinger, 1860	= <i>Pseudonaja</i>
<i>christianus</i> , <i>Lunelaps</i> , Worrell, 1963	= <i>Furina ornata</i>	<i>fasciata</i> , <i>Denisonia</i> , Rosen, 1905	= <i>Denisonia fasciata</i>
<i>christianus</i> , <i>Pseudelaps</i> , Fry, 1915	= <i>Furina ornata</i>	<i>fasciata</i> , <i>Vermicella</i> , Stirling & Zietz, 1893	= <i>Simoselaps fasciolatus</i>
<i>collaris</i> , <i>Hoplocephalus</i> , Macleay, 1887	= <i>Drysdalia mastersii</i>	<i>fasciolata</i> , <i>Alecto</i> , Jan, 1863	= <i>Notechis scutatus</i>
<i>colletti</i> , <i>Pseudechis</i> , Boulenger, 1902	= <i>Pseudechis colletti</i>	<i>fasciolatus</i> , <i>Rhinelaps</i> , Günther, 1872	= <i>Simoselaps fasciolatus</i>
<i>coronatus</i> , <i>Elaps</i> , Schlegel, 1837	= <i>Drysdalia coronata</i>	<i>fenestrata</i> , <i>Denisonia</i> , DeVis, 1905	= <i>Glyphodon tristis</i>
<i>coronoides</i> , <i>Hoplocephalus</i> , Günther, 1858	= <i>Drysdalia coronoides</i>	<i>ferox</i> , <i>Diemenia</i> , Macleay, 1882	= <i>Oxyuranus (Parademansia)</i> <i>microlepidota</i>
<i>Cryptophis</i> Worrell, 1961	= <i>Cryptophis</i>	<i>flagellum</i> , <i>Hoplocephalus</i> , McCoy, 1867	= <i>Unechis flagellum</i>
<i>cucullata</i> , <i>Diemansia</i> , Günther, 1862	= <i>Cacophis squamulosus</i>	<i>flavicollis</i> , <i>Cacophis harriet-</i> <i>tae</i> , McDowell, 1967	= <i>Cacophis harriettae</i>
<i>cucullata</i> , <i>Furina</i> , Boulenger, 1896	= <i>Pseudonaja textilis</i>	<i>fordei</i> , <i>Cacophis</i> , Krefft, 1869	= <i>Cacophis krefftii</i>
<i>cupreiceps</i> , <i>Demansia reticu-</i> <i>lata</i> , Storr, 1978	= <i>Demansia reticulata</i>	<i>forresti</i> , <i>Denisonia</i> , Boulenger, 1906	= <i>Suta suta</i>
<i>cupreus</i> , <i>Pseudechis</i> , Boulenger, 1896	= <i>Pseudechis australis</i>	<i>frenatus</i> , <i>Hoplocephalus</i> , Peters, 1870	= <i>Suta suta</i>
<i>cupreus</i> , <i>Pseudechis</i> , Boulenger, 1896	= <i>Pseudonaja textilis</i>	<i>frontalis</i> , <i>Hoplocephalus</i> , Ogilby, 1890	= <i>Suta suta</i>
<i>curta</i> , <i>Naja</i> , Schlegel, 1837	= <i>Echiopsis curta</i>	<i>Furina</i> Duméril, 1853	= <i>Furina</i>
<i>cuvieri</i> , <i>Oplocephalus</i> , Gray, 1831	= <i>Notechis scutatus</i>	<i>fuscicollis</i> , <i>Rhynchelaps</i> , Lönnberg & Andersson, 1915	= <i>Simoselaps warro</i>
<i>daemeli</i> , <i>Denisonia</i> , Boulenger, 1896	= <i>Hemiaspis damelii</i>	<i>fuscus</i> , <i>Hoplocephalus</i> , Steindachner, 1867	= <i>Notechis scutatus</i>
<i>damelii</i> , <i>Hoplocephalus</i> , Günther, 1876	= <i>Hemiaspis damelii</i>	<i>Glyphodon</i> Günther, 1858	= <i>Furina</i>
<i>darwiniensis</i> , <i>Pseudechis</i> , Macleay, 1878	= <i>Pseudechis australis</i>	<i>Glyphodon</i> Günther, 1858	= <i>Glyphodon</i>
<i>Demansia</i> Günther, 1858	= <i>Demansia</i>	<i>gouldii</i> , <i>Elaps</i> , Gray, 1841	= <i>Unechis gouldii</i>
<i>Denisonia</i> Krefft, 1869	= <i>Denisonia</i>	<i>guntheri</i> , <i>Cacophis</i> , Steindachner, 1867	= <i>Pseudonaja textilis</i>
<i>denisonioides</i> , <i>Pseudechis</i> , Werner, 1909	= <i>Pseudechis australis</i>	<i>guttata</i> , <i>Demansia</i> , Parker, 1926	= <i>Pseudonaja guttata</i>
<i>devisi</i> , <i>Denisonia maculata</i> , Waite & Longman, 1920	= <i>Denisonia devisii</i>	<i>guttata</i> , <i>Pseudechis</i> , DeVis 1905	= <i>Pseudechis guttatus</i>
<i>diadema</i> , <i>Brachysoma</i> , Schlegel, 1837	= <i>Neelaps bimaculata</i>	<i>harriettae</i> , <i>Cacophis</i> , Krefft, 1869	= <i>Cacophis harriettae</i>
<i>diadema</i> , <i>Calamaria</i> , Schlegel, 1837	= <i>Furina diadema</i>	<i>Hemiaspis</i> Fitzinger, 1860	= <i>Hemiaspis</i>
<i>Diemansia</i> Günther, 1858	= <i>Demansia</i>	<i>Homaloselaps</i> Jan, 1858	= <i>Vermicella</i>
<i>Diemenia</i> Günther, 1863	= <i>Demansia</i>	<i>Hoplocephalus</i> Wagler, 1830	= <i>Hoplocephalus</i>
<i>Diemennia</i> Günther, 1863	= <i>Demansia</i>	<i>Hornea</i> Lucas & Frost, 1896	= <i>Simoselaps</i>
<i>dorsalis</i> , <i>Alecto</i> , Jan, 1863	= <i>Unechis nigrostriatus</i>	<i>humphreysi</i> , <i>Notechis ater</i> , Worrell, 1963	= <i>Notechis ater humphreysi</i>
<i>Drepanodontis</i> Worrell, 1961	= <i>Hemiaspis</i>	<i>incincta</i> , <i>Vermicella</i> <i>semifasciata</i> , Storr, 1968	= <i>Simoselaps incinctus</i>
<i>Drysdalia</i> Worrell, 1961	= <i>Drysdalia</i>	<i>inframacula</i> , <i>Demansia</i> <i>textilis</i> , Waite, 1925	= <i>Pseudonaja textilis</i>
<i>dunmalli</i> , <i>Glyphodon</i> , Worrell, 1955	= <i>Glyphodon dunmalli</i>	<i>ingrami</i> , <i>Diemenia</i> , Boulenger, 1908	= <i>Pseudonaja nuchalis</i>
<i>dwyeri</i> , <i>Denisonia</i> , Worrell, 1956	= <i>Unechis dwyeri</i>	<i>kubingii</i> , <i>Pseudoelaps</i> , Jan, 1859	= <i>Pseudonaja textilis</i>
<i>Echiopsis</i> Fitzinger, 1843	= <i>Echiopsis</i>	<i>kubinyi</i> , <i>Pseudoelaps</i> , Jan, 1863	= <i>Pseudonaja textilis</i>
<i>Elapidocephalus</i> Macleay, 1884	= <i>Demansia</i>	<i>labialis</i> , <i>Alecto</i> , Jan, 1859	= <i>Austrelaps superbus</i>
<i>Elapocephalus</i> Macleay, 1878	= <i>Demansia</i>		
<i>Elapocormus</i> Fitzinger, 1843	= <i>Hoplocephalus</i>		
<i>Elapocranium</i> Macleay, 1878	= <i>Demansia</i>		

- labialis*, *Alecto*, Jan & Sordelli, 1873 = *Drysdalia coronoides*
laevis, *Acanthophis*, Macleay, 1878 = *Acanthophis antarcticus*
laevis, *Boa* = incertae sedis
latizonatus, *Rhynchelaps*, DeVis, 1905 = *Vermicella annulata*
leptocephalus, *Trimeresurus*, Lacépède, 1804 = *Pseudechis porphyriacus*
littoralis, *Vermicella bert-holdi*, Storr, 1968 = *Simoselaps littoralis*
Lunelaps Worrell, 1961 = *Furina*
lunulata, *Vermicella*, Krefft, 1869 = *Vermicella annulata*
maclennani, *Oxyuranus*, Kinghorn, 1923 = *Oxyuranus scutellatus*
maculatus, *Hoplocephalus*, Steindachner, 1867 = *Denisonia maculata*
maculiceps, *Diemenia*, Boettger, 1898 = *Demansia atra*
Mainophis Macleay, 1877 = *Glyphodon*
mastersii, *Hoplocephalus*, Krefft, 1866 = *Drysdalia mastersii*
mattozoi, *Elaps*, Ferreira, 1891 = *Simoselaps bertholdi*
melaena, *Demansia papuen-sis*, Storr, 1978 = *Demansia papuensis*
melanocephalus, *Elaps*, Gray & Neill, 1845 = *Drysdalia coronata*
melanotus, *Alecto*, Jan, 1863 = *Cryptophis nigrescens*
Melwardia Worrell, 1960 = *Simoselaps*
microlepidota, *Diemenia*, McCoy, 1879 = *Oxyuranus (Parademansia) microlepidota*
minima, *Melwardia*, Worrell, 1960 = *Simoselaps minimus*
minor, *Hoplocephalus*, Günther, 1863 = *Elapognathus minor*
minutus, *Pseudelaps*, Fry, 1915 = *Drysdalia rhodogaster*
modesta, *Cacophis*, Günther, 1875 = *Pseudonaja modesta*
monachus, *Denisonia*, Storr, 1964 = *Unechis monachus*
mortonensis, *Pseudechis*, DeVis, 1911 = *Pseudechis guttatus*
muelleri, *Hoplocephalus*, Fischer, 1885 = *Denisonia maculata*
multifasciata, *Furina*, Longman, 1915 = *Vermicella multifasciata*
Narophis Worrell, 1961 = *Neelaps*
Neelaps Günther, 1863 = *Neelaps*
neocaledonicus, *Neelaps*, Palacky, 1898 = *Neelaps calonotus*
niger, *Notechis scutatus*, Kinghorn, 1921 = *Notechis ater*
nigra, *Denisonia*, DeVis, 1905 = *Drysdalia coronoides*
nigrescens, *Hoplocephalus*, Günther, 1862 = *Cryptophis nigrescens*
nigriceps, *Hoplocephalus*, Günther, 1863 = *Unechis nigriceps*
nigrostriatus, *Hoplocephalus*, Krefft, 1864 = *Unechis nigrostriatus*
Notechis Boulenger, 1896 = *Notechis*
nuchalis, *Pseudonaja*, Günther, 1858 = *Pseudonaja nuchalis*
nullarbor, *Denisonia spectabilis*, Storr, 1981 = *Unechis spectabilis*
occidentalis, *Notechis scuta-tus*, Glauert, 1948 = *Notechis scutatus*
occipitale, *Rabdion*, Girard, 1858 = *Furina diadema*
occipitalis, *Elaps*, Duméril, Bibron & Duméril, 1854 = *Vermicella annulata*
olivaceus, *Lycodon*, Gray, 1842 = *Demansia olivacea*
olivaceus, *Trimeresurus*, Gray, 1841 = *Drysdalia coronata*
Ophrias Cuvier, 1829 = *Acanthophis*
Ophryas Merrem, 1820 = *Acanthophis*
Oplocephalus Gray, 1831 = *Hoplocephalus*
ornata, *Denisonia*, Krefft, 1869 = *Denisonia maculata*
ornaticeps, *Elapocephalus*, Macleay, 1878 = *Demansia olivacea*
ornatus, *Elaps*, Gray, 1842 = *Furina diadema*
ornatus, *Hoplocephalus*, DeVis, 1884 = *Denisonia devisii*
Oxyuranus Kinghorn, 1923 = *Oxyuranus*
pallidiceps, *Hoplocephalus*, Günther, 1858 = *Cryptophis pallidiceps*
palpebrosa, *Boa*, Shaw, 1802 = *Acanthophis antarcticus*
papuensis, *Diemenia*, Macleay, 1877 = *Demansia papuensis*
Parasuta Worrell, 1961 = *Unechis*
Parademansia Kinghorn, 1955 = *Oxyuranus*
permixta, *Alecto*, Jan, 1863 = *Cryptophis nigrescens*
Petrodymon Krefft, 1866 = *Cacophis*
platycephalus, *Pseudechis*, Thomson, 1933 = *Pseudechis australis*
porphyraicus, *Pseudechis*, McCoy, 1867 = *Pseudechis porphyriacus*
porphyriacus, *Coluber*, Shaw, 1794 = *Pseudechis porphyriacus*
prophyrica, *Naja*, Schlegel, 1837 = *Pseudechis porphyriacus*
praelongus, *Acanthophis*, Ramsay, 1877 = *Acanthophis praelongus*
propinqua, *Denisonia frontalis*, DeVis, 1905 = *Suta suta*
psammophidius, *Pseudelaps*, Duméril, Bibron & Duméril, 1854 = *Demansia psammophis*
psammophis, *Elaps*, Schlegel, 1837 = *Demansia psammophis*
Pseuäechis Wagler, 1830 = *Pseudechis*
Pseudechys Stirling & Zietz, 1893 = *Pseudechis*
Pseudonaja Günther, 1858 = *Pseudonaja*
pulchella, *Hornea*, Lucas & Frost, 1896 = *Simoselaps fasciolatus*
punctata, *Denisonia*, Boulenger, 1896 = *Denisonia punctata*
pyrrhus, *Acanthophis*, Boulenger, 1898 = *Acanthophis pyrrhus*

- ramsayi*, Furina, Macleay, 1885 = *Pseudonaja modesta*
ramsayi, *Hoplocephalus*, Krefft, 1864 = *Austrelaps superbus*
reticulatus, *Lycodon*, Gray, 1842 = *Demansia psammophis*
revelata, *Denisonia*, DeVis, 1911 = *Hoplocephalus bitorquatus*
Rhinelaps Günther, 1872 = *Simoselaps*
Rhinoplocephalus Boulenger, 1896 = *Rhinoplocephalus*
Rhinoplocephalus Müller, 1885 = *Rhinoplocephalus*
rhinostomus, *Pseudelaps*, Jan & Sordelli, 1873 = *Simoselaps semifasciatus*
rhodogaster, *Alecto*, Jan, 1863 = *Drysdalia rhodogaster*
Rhynchelaps Boulenger, 1896 = *Simoselaps*
Rhynchoelaps Jan, 1858 = *Simoselaps*
robusta, Furina, DeVis, 1905 = *Simoselaps bertholdi*
robusta, *Mainophis*, Macleay, 1877 = *Glyphodon tristis*
roperi, *Rhynchoelaps*, Kinghorn, 1931 = *Simoselaps semifasciatus*
rostralis, *Denisonia*, DeVis, 1911 = *Simoselaps warro*
rufescens, *Demansia olivacea*, Storr, 1978 = *Demansia olivacea*
rugosus, *Acanthophis antarcticus*, Loveridge, 1948 = *Acanthophis praelongus*
schmidtii, *Alecto*, Jan & Sordelli, 1873 = *Austrelaps superbus*
scutata, *Naja (Hemadryas)*, Peters, 1861 = *Notechis scutatus*
scutellatus, *Pseudechis*, Peters, 1867 = *Oxyuranus scutellatus*
semifasciata, *Brachyurophis*, Günther, 1863 = *Simoselaps semifasciatus*
serventyi, *Notechis ater*, Worrell, 1963 = *Notechis ater serventyi*
signata, *Alecto*, Jan, 1859 = *Hemiaspis signata*
simile, *Brachysoma*, Macleay, 1878 = *Furina diadema*
Simoselaps, Jan, 1859 = *Simoselaps*
simplex, *Demansia*, Storr, 1978 = *Demansia simplex*
smithii, *Rhynchoelaps*, Kinghorn, 1931 = *Simoselaps semifasciatus*
snelli, *Vermicella annulata*, Storr, 1968 = *Vermicella annulata*
sorda, *Viper*, Salvado, 1851 = *Acanthophis antarcticus*
sordellii, *Pseudelaps*, Jan, 1859 = *Pseudonaja textilis*
sp., *Glyphodon*, Worrell, 1963 = *Cacophis harriettae*
spectabilis, *Hoplocephalus*, Krefft, 1869 = *Unechis spectabilis*
squamulosus, *Pseudelaps*, Duméril, 1853 = *Cacophis squamulosus*
stephensii, *Hoplocephalus*, Krefft, 1869 = *Hoplocephalus stephensii*
stirlingi, *Hoplocephalus*, Lucas & Frost, 1896 = *Suta suta*
suboccipitalis, *Hoplocephalus*, Ogilby, 1892 = *Hemiaspis damelii*
sulcans, *Hoplocephalus*, DeVis, 1884 = *Hoplocephalus bitorquatus*
Superbus, *Hoplocephalus*, Günther, 1858 = *Austrelaps superbus*
superbus, *Hoplocephalus*, Günther, 1858 = *Elapognathus minor*
superciliaris, *Diemenia*, McCoy, 1867 = *Pseudonaja textilis*
superciliosus, *Pseudoelaps*, Fischer, 1856 = *Pseudonaja textilis*
Suta Worrell, 1961 = *Suta*
sutherlandi, *Brachysoma*, DeVis, 1884 = *Pseudonaja nuchalis*
sutus, *Hoplocephalus*, Peters, 1863 = *Suta suta*
tanneri, *Demansia nuchalis*, Worrell, 1961 = *Pseudonaja affinis*
temporalis, *Hoplocephalus*, Günther, 1862 = *Echiopsis curta*
textilis, Furina, Duméril, Bibron & Duméril, 1854 = *Pseudonaja textilis*
torquata, *Diemansia*, Günther, 1862 = *Demansia torquata*
tortor, *Acanthophis*, Lesson, 1829-1831 = *Pseudechis porphyriacus*
tristis, *Glyphodon*, Günther, 1858 = *Glyphodon tristis*
Tropidechis Günther, 1863 = *Tropidechis*
Unechis Worrell, 1961 = *Unechis*
vagrans, *Denisonia*, Garman, 1901 = *Hemiaspis signata*
variegata, *Alecto*, Duméril, Bibron & Duméril, 1854 = *Hoplocephalus bungaroides*
Vermicalla Günther, 1858 = *Vermicella*
Vermicella Günther, 1858 = *Vermicella*
vestigatus, *Hoplocephalus*, DeVis, 1884 = *Demansia atra*
waitii, *Hoplocephalus*, Ogilby, 1894 = *Hoplocephalus bitorquatus*
warro, *Cacophis*, DeVis, 1884 = *Simoselaps warro*
wilesmithii, *Pseudechis*, DeVis, 1911 = *Oxyuranus scutellatus*
woodjonesii, *Rhynchelaps*, Thomson, 1934 = *Simoselaps semifasciatus*

Marine Proteroglyphs

- abbreviatus*, *Hydrophis*, Jan, 1863 = *Lapemis hardwickii*
Acalyptophis Boulenger, 1896 = *Acalyptophis*
Acalyptus Duméril, 1853 = *Acalyptophis*
Aepyurus Agassiz, 1846 = *Aipysurus*
affinis, *Platurus*, Anderson, 1871 = *Laticauda laticaudata*
Aipysurus Lacépède, 1804 = *Aipysurus*
alcocki, *Hydrophis*, Wall, 1906 = *Hydrophis atriceps*

- alternans*, *Hydrophis*
(*Pelamis*) *bicolor*,
Fischer, 1856 = *Pelamis platurus*
- andamanica*, *Distira*,
Annandale, 1905 = *Hydrophis ornatus*
- anguillaeformis*,
Thalassophis, Schmidt,
1852 = *Aipysurus eydouxii*
- annulata*, *Hydrophis*
(*Pelamis*) *pelamidoides*,
Fischer, 1856 = *Lapemis hardwickii*
- annulatus*, *Emydocephalus*
Krefft, 1869 = *Emydocephalus annulatus*
- annulatus*, *Hydrus*, Gray,
1849 = *Astrotia stokesii*
- annulatus*, *Polyodontes*,
Lesson, 1834 = *Hydrophis caerulescens*
- apraefrontalis*, *Aipysurus*,
M.A. Smith, 1926 = *Aipysurus apraefrontalis*
- Aspisurus* Gray, 1841 = *Aipysurus*
- Aturia* Gray, 1842 = *Hydrophis*
- Astrotia* Fischer, 1856 = *Astrotia*
- Asturia* Gray, 1842 = *Hydrophis*
- atriceps*, *Hydrophis*,
Günther, 1864 = *Hydrophis atriceps*
- australis*, *Aipysurus*,
Sauvage, 1877 = *Aipysurus duboisii*
- belcheri*, *Aturia*, Gray,
1849 = *Hydrophis belcheri*
- bengalensis*, *Hydrophis*,
Gray, 1842 = *Enhydrina schistosa*
- bicolor*, *Hydrus*, Schneider,
1799 = *Pelamis platurus*
- brevis*, *Hydrophis*, Jan,
1863 = *Lapemis hardwickii*
- caerulescens*, *Hydrus*,
Shaw, 1802 = *Hydrophis caerulescens*
- chelonicephalus*, *Aipysurus*,
Bavay, 1869 = *Emydocephalus annulatus*
- Chitulia* Gray, 1849 = *Hydrophis*
- cinninnatii*, *Disteira*, Van
Denburgh &
Thompson, 1908 = *Hydrophis atriceps*
- cloris*, *Hydrophis*, Daudin,
1803 = *Hydrophis obscurus*
- colubrinus*, *Hydrus*,
Schneider, 1799 = *Laticauda colubrina*
- coronata*, *Hydrophis*,
Günther, 1864 = *Hydrophis obscurus*
- cyanosoma*, *Distira*, Wall,
1913 = *Hydrophis inornatus*
- darwiniensis*, *Hydrelaps*,
Boulenger, 1896 = *Hydrelaps darwiniensis*
- Disteira* Lacépède, 1804 = *Disteira*
- Distira* Boulenger, 1896 = *Disteira*
- doliata*, *Disteira*, Lacépède,
1804 = *Disteira major*
- Dolichodira* Wall, 1921 = *Hydrophis*
- duboisii*, *Aipysurus*, Bavay,
1869 = *Aipysurus duboisii*
- dumerilii*, *Disteira*, Jan,
1859 = *Disteira major*
- elegans*, *Aturia*, Gray, 1842 = *Hydrophis elegans*
- elliotti*, *Hydrophis*, Günther,
1864 = *Hydrophis ornatus*
- Emydocephalus* Krefft,
1869 = *Emydocephalus*
- Enhydrina* Gray, 1849 = *Enhydrina*
- Ephalophis* M.A. Smith,
1931 = *Ephalophis*
- eydouxii*, *Tomogaster*,
Gray, 1849 = *Aipysurus eydouxii*
- fasciata*, *Chitulia*, Gray,
1849 = *Hydrophis inornatus*
- fischeri*, *Platurus*, Jan,
1859 = *Laticauda laticaudata*
- floweri*, *Hydrophis*,
Boulenger, 1898 = *Hydrophis melanosoma*
- foliosquama*, *Aipysurus*,
M.A. Smith, 1926 = *Aipysurus foliosquama*
- frontalis*, *Hydrophis*, Jan,
1863 = *Hydrophis caerulescens*
- frontalis*, *Platurus*, DeVis,
1905 = *Laticauda colubrina*
- fuliginosus*, *Aipysurus*,
Duméril, Bibron &
Duméril, 1854 = *Aipysurus laevis*
- fusca*, *Stephanohydra*,
Tschudi, 1837 = *Aipysurus fuscus*
- godeffroyi*, *Hydrophis*,
Peters, 1872 = *Hydrophis ornatus*
- gracilis*, *Hydrus*, Shaw,
1802 = *Hydrophis gracilis*
- grandis*, *Distira*, Boulenger,
1896 = *Hydrophis elegans*
- granosa*, *Hydrophis*,
Anderson, 1871 = *Astrotia stokesii*
- greyi*, *Ephalophis*, M.A.
Smith, 1931 = *Ephalophis greyi*
- guentheri*, *Hydrophis*,
Theobald, 1868 = *Astrotia stokesii*
- guntheri*, *Hydrophis*,
Murray, 1884 = *Hydrophis gracilis*
- guttata*, *Hydrophis*,
Murray, 1887 = *Astrotia stokesii*
- hardwickii*, *Lapemis*, Gray,
1835 = *Lapemis hardwickii*
- horrida*, *Pseudodistira*,
Kinghorn, 1926 = *Acalyptophis peronii*
- hybrida*, *Hydrophis*,
Schlegel, 1844 = *Hydrophis caerulescens*
- Hydrelaps* Boulenger,
1896 = *Hydrelaps*
- Hydrophis* Sonnini de
Manoncourt &
Latreille, 1802 = *Hydrophis*
- Hypotropis* Gray, 1846 = *Aipysurus*
- inornata*, *Chitulia*, Gray,
1849 = *Hydrophis inornatus*
- jukesii*, *Hypotropis*, Gray,
1846 = *Aipysurus laevis*
- kadellnagam*, *Hydrophis*,
Boie, 1827 = *Hydrophis gracilis*
- kingii*, *Hydrophis*,
Boulenger, 1896 = *Disteira kingii*
- Kolpophis* M.A. Smith,
1926 = *Lapemis*
- lacepedei*, *Hydrophis*, Jan,
1859 = *Disteira major*
- laevis*, *Aipysurus*, Lacépède,
1804 = *Aipysurus laevis*

<i>laevis</i> , <i>Hydrophis</i> , Lütken, 1863	= <i>Hydrophis ornatus</i>	<i>pachycercos</i> , <i>Hydrophis</i> , Fischer, 1856	= <i>Hydrophis belcheri</i>
<i>Lapemis</i> Gray, 1835	= <i>Lapemis</i>	<i>pachycerios</i> , <i>Hydrophis</i> , Jan, 1859	= <i>Hydrophis belcheri</i>
<i>Laticauda</i> Laurenti, 1768	= <i>Laticauda</i>	<i>pacificus</i> , <i>Hydrophis</i> , Boulenger, 1896	= <i>Hydrophis pacificus</i>
<i>laticaudatus</i> , <i>Coluber</i> , Linnaeus, 1758	= <i>Laticauda laticaudata</i>	<i>Parahydrophis</i> Burger & Natsuno, 1974	= <i>Parahydrophis</i>
<i>laticaudatus</i> , <i>Coluber</i> , Linnaeus, 1758	= <i>Laticauda colubrina</i>	<i>pelamidooides</i> , <i>Hydrophis</i> , Schlegel, 1837	= <i>Lapemis hardwickii</i>
<i>latifasciata</i> , <i>Hydrophis</i> , Günther, 1864	= <i>Hydrophis obscurus</i>	<i>Pelamis</i> Daudin, 1803	= <i>Pelamis</i>
<i>laurenti</i> , <i>Platurus</i> , Rafinesque, 1817	= <i>Laticauda laticaudata</i>	<i>pelamis</i> , <i>Hydrophis</i> , Schlegel, 1837	= <i>Pelamis platurus</i>
<i>Leioselasma</i> Lacépède, 1804	= <i>Hydrophis</i>	<i>pelamoides</i> , <i>Hydrophis</i> , Hilgendorf, 1876	= <i>Lapemis hardwickii</i>
<i>leprogaster</i> , <i>Hydrophis</i> , Duméril & Bibron, 1856	= <i>Hydrophis gracilis</i>	<i>Pelamydrus</i> Stejneger, 1910	= <i>Pelamis</i>
<i>Liopala</i> Gray, 1842	= <i>Hydrophis</i>	<i>peronii</i> , <i>Acalyptus</i> , Duméril, 1853	= <i>Acalyptophis peronii</i>
<i>Liopola</i> Gray, 1842	= <i>Hydrophis</i>	<i>platura</i> , <i>Anguis</i> , Linnaeus, 1766	= <i>Pelamis platurus</i>
<i>longiceps</i> , <i>Hydrophis</i> , Günther, 1864	= <i>Hydrophis inornatus</i>	<i>Platurus</i> Sonnini de Manoncourt & Latreille, 1802	= <i>Laticauda</i>
<i>loreatus</i> , <i>Lapemis</i> , Gray, 1843	= <i>Lapemis hardwickii</i>	<i>platycaudatus</i> , <i>Coluber</i> , Oken, 1836	= <i>Laticauda colubrina</i>
<i>lubricus</i> , <i>Pelagophis</i> , Peters & Doria, 1878	= <i>Aipysurus duboisii</i>	<i>Platyurus</i> Agassiz, 1846	= <i>Laticauda</i>
<i>macfarlani</i> , <i>Distira</i> , Boulenger, 1896	= <i>Hydrophis cyanocinctus</i>	<i>Polydontognathus</i> Wall, 1921	= <i>Hydrophis</i>
<i>maculata</i> , <i>Hydrophis</i> <i>bicolor</i> , Jan, 1863	= <i>Pelamis platurus</i>	<i>polydonta</i> , <i>Hydrophis</i> , Jan, 1863	= <i>Hydrophis caerulescens</i>
<i>major</i> , <i>Hydrus</i> , Shaw, 1802	= <i>Disteira major</i>	<i>Polypholophis</i> Wall, 1921	= <i>Hydrophis</i>
<i>major</i> , <i>Hydrus</i> , Shaw, 1802	= <i>Astrotia stokesii</i>	<i>pooleorum</i> , <i>Aipysurus laevis</i> , L.A. Smith, 1974	= <i>Aipysurus laevis</i>
<i>manillae</i> , <i>Hydrophis</i> , Owen, 1859	= <i>Hydrophis inornatus</i>	<i>Porrecticollis</i> Wall, 1921	= <i>Hydrophis</i>
<i>margaritophorus</i> , <i>Aipysurus</i> , Bleeker, 1858	= <i>Aipysurus eydouxii</i>	<i>Praescutata</i> Wall, 1921	= <i>Lapemis</i>
<i>melanocephala</i> , <i>Hydrophis</i> <i>sublaevis</i> , Gray, 1849	= <i>Hydrophis melanocephalus</i>	<i>problematicus</i> , <i>Hydrophis</i> , Jan, 1859	= <i>Lapemis hardwickii</i>
<i>Melanomystax</i> Wall, 1921	= <i>Disteira</i>	<i>protervus</i> , <i>Hydrophis</i> , Jan, 1859	= <i>Hydrophis caerulescens</i>
<i>melanosoma</i> , <i>Hydrophis</i> , Günther, 1864	= <i>Hydrophis melanosoma</i>	<i>Pseudodistira</i> Kinghorn, 1926	= <i>Acalyptophis</i>
<i>mentalis</i> , <i>Hydrophis</i> , Gray, 1842	= <i>Disteira major</i>	<i>rostralis</i> , <i>Hydrophis</i> , M.A. Smith, 1917	= <i>Hydrophis gracilis</i>
<i>mertoni</i> , <i>Distira</i> , Roux, 1910	= <i>Parahydrophis mertoni</i>	<i>russellii</i> , <i>Disteira</i> , Fitzinger, 1827	= <i>Enhydrina schistosa</i>
<i>microcephalus</i> , <i>Hydrophis</i> , Lesson, 1834	= <i>Hydrophis gracilis</i>	<i>schneideri</i> , <i>Pelamis</i> , Rafinesque, 1817	= <i>Pelamis platurus</i>
<i>microcephala</i> , <i>Thalassophis</i> , Schmidt, 1852	= <i>Hydrophis gracilis</i>	<i>schistosus</i> , <i>Hydrophis</i> , Daudin, 1803	= <i>Enhydrina schistosa</i>
<i>Micromastophis</i> Wall, 1921	= <i>Hydrophis</i>	<i>schistotus</i> , <i>Hydrophis</i> , Jan, 1859	= <i>Enhydrina schistosa</i>
<i>mjobergi</i> , <i>Distira</i> , Lönnberg & Andersson, 1913	= <i>Hydrophis ornatus</i>	<i>schizopholis</i> , <i>Hydrophis</i> , Schmidt, 1846	= <i>Astrotia stokesii</i>
<i>muelleri</i> , <i>Platurus</i> , Boulenger, 1896	= <i>Laticauda laticaudata</i>	<i>schlegelii</i> , <i>Thalassophis</i> , Schmidt, 1852	= <i>Hydrophis inornatus</i>
<i>muraeniformis</i> , <i>Thalassophis</i> , Schmidt, 1852	= <i>Aipysurus eydouxii</i>	<i>scutata</i> , <i>Laticauda</i> , Laurenti, 1768	= <i>Laticauda laticaudata</i>
<i>nasalis</i> , <i>Distira</i> , DeVis, 1905	= <i>Disteira major</i>	<i>shavii</i> , <i>Pelamis</i> , Merrem, 1820	= <i>Disteira major</i>
<i>obscura</i> , <i>Hydrophis</i> , Daudin, 1803	= <i>Hydrophis obscurus</i>	<i>sinuata</i> , <i>Pelamis bicolor</i> , Duméril, Bibron & Duméril, 1854	= <i>Pelamis platurus</i>
<i>ocellata</i> , <i>Hydrophis</i> , Gray, 1849	= <i>Hydrophis ornatus</i>	<i>Stephanohydra</i> Tschudi, 1837	= <i>Aipysurus</i>
<i>orientalis</i> , <i>Disteira</i> , Stejneger, 1901	= <i>Hydrophis melanocephalus</i>	<i>stokesii</i> , <i>Hydrus</i> , Gray, 1846	= <i>Astrotia stokesii</i>
<i>ornata</i> , <i>Aturia</i> , Gray, 1842	= <i>Hydrophis ornatus</i>		
<i>ornata</i> , <i>Pelamis</i> , Gray, 1842	= <i>Pelamis platurus</i>		

subcinctus, *Hydrophis*,
 Gray, 1842 = *Hydrophis obscurus*
subfasciata, *Hydrophis*,
 Gray, 1842 = *Enhydrina schistosa*
superciliosus, *Acalyptus*,
 Duméril, Bibron &
 Duméril, 1854 = *Acalyptophis peronii*
tenuis, *Aipysurus*, Lönnberg
 & Andersson, 1913 = *Aipysurus tenuis*
thai, *Hydrophis caerulescens*,
 M.A. Smith, 1920 = *Hydrophis caerulescens*
Thalassophina, M.A. Smith,
 1926 = *Lapemis*

Tomogaster Gray, 1849 = *Aipysurus*
trachyceps, *Hydrophis* = *Hydrophis cyanocinctus*
tuberculatus, *Emydoceph-*
alus, Krefft, 1869 = *Emydocephalus annulatus*
valakadyn, *Disteira*, Boie,
 1827 = *Enhydrina schistosa*
variegata, *Pelamis*, Duméril,
 Bibron & Duméril,
 1854 = *Pelamis platurus*
weneri, *Thalassophis*,
 Schmidt, 1852 = *Enhydrina schistosa*

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Sensory Papilla Patterns of the Cheek Lateralis System in the Gobiid Fishes *Acentrogobius* and *Glossogobius*, and Their Significance for the Classification of Gobioid Fishes

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ABSTRACT. The sensory papilla patterns of the cheek lateralis system are described and compared in various species of *Acentrogobius* and *Glossogobius*. Methods of studying and naming the papilla lines are discussed. Two basic patterns are recognized, a transverse pattern with several vertical papilla lines and two horizontal lines, and a longitudinal pattern with only horizontal lines. The significance of the orientation of the papillae within the lines and the development of ridges connecting the papillae in determining homologies is discussed. It is suggested that the transverse papilla pattern has developed independently in *Glossogobius circumspectus* and *Acentrogobius viridipunctatus* from structurally different longitudinal patterns.

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Almost all gobioid fishes have lateralis system sensory papillae or free neuromasts on the head and body outside the head canals. The papillae are developed as small bumps, arising from the skin, sometimes on large flaps, arranged in characteristic lines or rows. Their importance in the classification of gobioid fishes has long been recognized by European and Japanese workers (Sanzo, 1911; Aurich, 1938; Miller & Wongratana, 1979; Akihito & Meguro, 1975; Takagi, 1957).

Generally two distinctive patterns have been recognized (Aurich, 1938). In the transverse pattern the cheek and preopercular papillae are developed in two horizontal and four or more vertical lines (Fig. 1). In the longitudinal pattern the papillae are arranged only in more or less horizontal lines (Fig. 2). Considerable variation occurs in these patterns, but by examining the arrangement of the lines and the orientation of the papillae within these lines, it is possible to group all gobiids within one or the other pattern type, with the exception of species with a very reduced number of papillae.

Some workers have simply illustrated the papilla patterns (Hoesé & Allen, 1977; Aurich, 1938; Takagi, 1957), but others have labelled the various lines with numerical or alphabetical characters. At present no standardization exists. Akihito & Meguro (1975, 1977, 1980) numbered all the papilla lines, beginning at the snout, without discriminating between the vertical and

horizontal lines. This system has considerable internal consistency when dealing with species in the same genus. It has a disadvantage in comparisons of genera with different patterns, since the same lines in different genera often have different numbers. European workers (Miller, 1974; Miller & Wongratana, 1979; Iljin, 1930) have generally followed the nomenclature of Sanzo (1911). The work of Sanzo was the first detailed study of sensory papillae in gobioid fishes and is still a classic work. Sanzo numbered the vertical rows under the eye, beginning below the front of the eye, lettered the horizontal rows under the eye from a to d, and labelled other papilla rows with alphabetic characters, often using a prime mark to indicate branches of the various rows. This system offers the greatest potential for determining phylogeny. However, there are several disadvantages. The system was based on European gobiids and is often not easily applicable to the vast mosaic of patterns found among other gobiid fishes. For example, many Indo-Pacific genera have more than four horizontal cheek lines (a to d of Sanzo). Also, determining homologies in the various lines has often proved difficult.

Several questions exist regarding the transverse and longitudinal papilla patterns. It is not known which pattern, if either, is primitive, or whether either pattern is monophyletic. Since both patterns occur across conventional taxonomic groupings, one or both patterns would appear to be polyphyletic. However, it could be

argued that the patterns represent specializations indicating phylogenetic lines, since detailed phylogenies of gobioid fishes are largely unavailable. In the most primitive gobioid known, *Rhyacichthys*, there are numerous bumps, presumably the sensory papillae, evenly spaced on the head, but not arranged into lines. Although this pattern may be primitive, *Rhyacichthys* lives in very swift-flowing waters, and interpretation of the pattern is difficult.

An alternative test of the question of the inter-relationships of the patterns is to examine genera, as currently recognized, that have some species with the transverse pattern and others with the longitudinal pattern. Both patterns are well known in *Glossogobius* and *Acentrogobius*. In each genus, only one or two species have been recognized with the transverse pattern, while all other species recognized have the longitudinal pattern.

Methods and Materials

Methods. The following discussion of methods for studying the papillae is based on observations made over a period of 15 years.

Factors that affect the preservation and visibility of the papillae include (1) initial condition of the specimen, (2) initial fixation, (3) long term preservation fluid, (4) handling of the specimen, and (5) taxon involved.

- (1). The initial condition of a specimen is the most critical factor. Specimens should be preserved as soon as possible, with best results being obtained from specimens preserved within a few minutes of collection. Freezing or storing specimens on ice invariably leads to collapse of the papillae. Similarly, best results are obtained when specimens are isolated in large vials or plastic bags. Collecting gobies in nets full of larger fish rarely produces satisfactory results.
- (2). Standard fixation of gobies is generally adequate. Ten per cent formalin gives best results, but considerable latitude is possible. Specimens can be fixed for up to one hour in 20 to 30% formalin without damage to the papillae, if the specimens are then transferred to 10% formalin. Initial fixation in alcohol also gives reasonable results, but it is not recommended, since specimens often become dehydrated and brittle. Long fixation in formalin over 15% generally leads to dehydration, resulting in the collapse of the papillae. Fixation in formalin solutions of less than five per cent also is inadequate.
- (3). Long term storage in formalin (a year or more) appears to result in collapse of the papillae. Specimens preserved for several years in isopropyl alcohol also had collapsed papillae. In numerous isopropyl specimens studied, the skin had become soft and flaccid. Specimens stored in ethyl alcohol (55 to 70%) generally show little collapse. Papillae were easily seen in Rüppell and Valenciennes material collected in the early 1800's. Generally

storage in any solution which reduces the quality of the specimen will lead to a collapse of the papillae.

- (4). Specimens should never be allowed to dehydrate. Use of a fibre optics light source and brief soaking of specimens in water before study generally prevents dehydration. Rehydration techniques can sometimes restore the papillae if dehydration is not severe.
- (5). Finally, the papillae vary in size in different genera. Papillae are often more difficult to see in specimens with a light-coloured head.

Examination of papillae is typically difficult but possible when a properly preserved specimen is examined. Study of untreated specimens is most difficult, and rarely can all papillae on the head be seen. Published drawings of papilla patterns are often incomplete. Ability to see the papillae generally increases with experience. High magnification and proper use of a light source are also critical factors for improving ability to see the papillae. Shining a low intensity light from the side often improves the contrast, but considerable experimentation is necessary to achieve best results. Blowing air over the specimen to remove excess water can improve papilla visibility, but too much air flow can result in dehydration.

Studies are most easily carried out on specially treated specimens. Potassium permanganate can be used to stain the papillae, although success varies considerably. For this study, trypsin-cleared specimens (Taylor, 1967) stored in glycerine were used. Blowing air gently over the head and using transmitted light consistently gave good results, when properly fixed specimens were used. In many cases glycerine storage appeared to partly restore collapsed papillae. Little improvement was noted in poorly preserved material. Long term storage in glycerine does not appear to affect the papillae, although the longest storage period observed was about 15 years. The eyes should not be removed from glycerine specimens, since the papillae near the eye can be damaged.

Drawings of papillae were made from cleared and stained glycerine specimens, with the aid of a camera lucida. The axes of the papillae have been exaggerated. Counts of papillae were taken from cleared and stained material and well-preserved specimens.

Material examined. All material examined is deposited in the Australian Museum, Sydney (AMS), the California Academy of Sciences, San Francisco (CAS), or the Museum National d'Histoire Naturelle, Paris (MNHN). The number following the registration number indicates number of specimens, and numbers in parentheses indicate ranges of standard lengths in mm. *Acentrogobius janthinopterus* (Bleeker): AMS I.19468-045, 1(47); I.20978-014, 2(27-66); I.22724, 1(41), all from Lizard Island, Queensland. *Acentrogobius therenzieni* Kiener: MNHN 1968-163 (holotype), Madagascar. *Acentrogobius viridipunctatus* (Valenciennes): AMS I.22090-006, 5(20-50), Salonika Beach, Queensland; AMS I.22720-010, 2(36-50), Townsville,

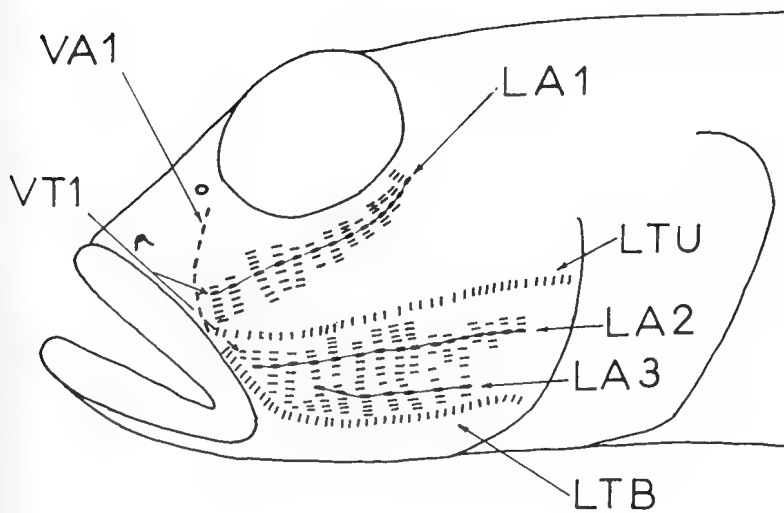


Fig. 1. Transverse sensory papilla pattern in *Acentrogobius viridipunctatus*, 49 mm SL. Cheek papillae only shown. Thin line connecting papillae indicates a very low ridge of skin. See text for meaning of abbreviations.

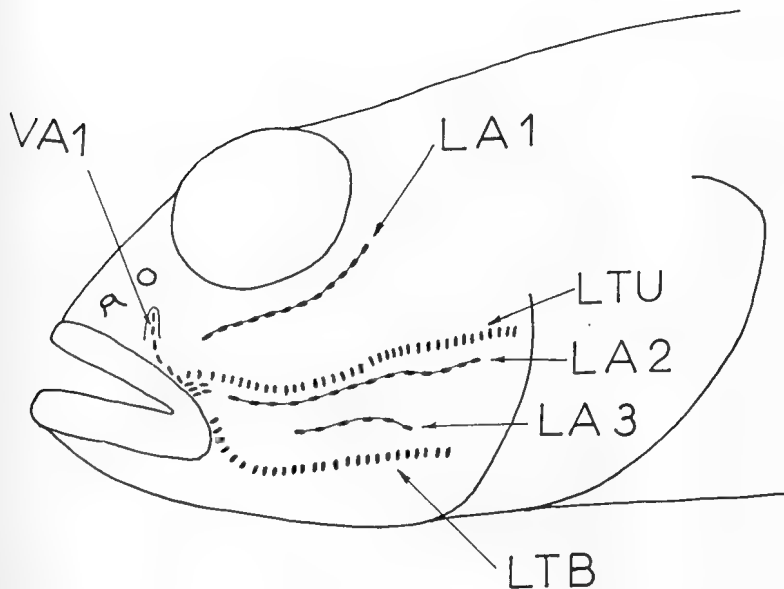


Fig. 2. Longitudinal sensory papilla pattern in *Acentrogobius janthinopterus*, 41 mm SL.

Queensland; AMS I.23265-001, 4(33-60); I.23279-002, 11(33-88), Weipa, Queensland. *Acentrogobius* sp.: AMS I.20124-004, 14(41-57), Port Stephens, New South Wales. *Glossogobius celebius* (Valenciennes): CAS, unregistered, 4(40-57), Palau; AMS I.21256-002, 11(17-43), Cape Tribulation, Queensland. *Glossogobius circumspectus* (Macleay): AMS I.22090-003, 22(24-113), Salonika Beach, Queensland; AMS I.22720, 1(49); I.23313-010, 2(68-92), Townsville, Queensland; AMS I.16670-016, 6(35-85), Madang, Papua New Guinea. *Glossogobius* sp.: AMS, unregistered, 3(45-52), Safia Creek, Papua New Guinea.

Terminology for Papillae

In almost all gobioid fishes each papilla is elongate, often elliptical in shape. The cheek papillae are arranged in distinct patterns in vertical, horizontal, or oblique rows or lines. These lines of papillae are typically referred to as pit lines (Takagi, 1957) or papilla rows.

The term papilla line is preferred here, since the papillae are rarely set in pits in gobioid fishes, and in some species each line can be composed of multiple rows of papillae. The axis of the papilla is oriented along the axis of the line or at right angles to the axis of the line.

Although several patterns occur in gobiid fishes, two distinct general patterns are recognizable: the transverse pattern and the longitudinal pattern. In the *transverse pattern* (Fig. 1) the cheek papillae are typically arranged in four or more vertical or slightly oblique rows extending from below the lower margin of the eye. There is an upper horizontal line (LTU) extending from under or behind the eye posteriorly on the preoperculum (the beginning of the line varying with the genus), and a lower horizontal line (LTB) extending from near the posterior end of the upper jaw. In the transverse pattern all the papillae are arranged with their elongate axes perpendicular to the axis of the line. In the *longitudinal pattern* (Fig. 2) there are four or more horizontal lines below the eye extending posteriorly on the preoper-

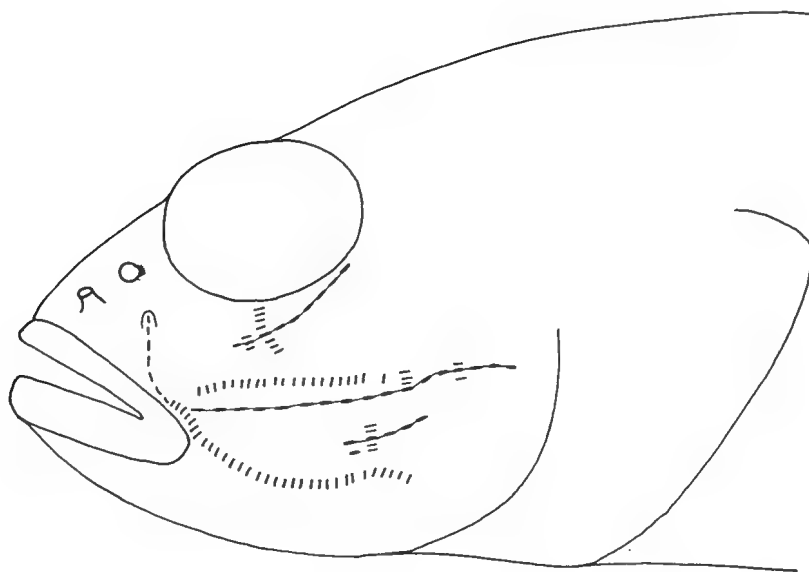


Fig. 3. Mixed sensory papilla pattern in *Acentrogobius* sp., 45 mm SL.

culum. There is a line extending from or just behind the middle of the upper jaw, along the lower margin of the eye, often ending at the infraorbital head pore (when present) behind the eye. Below this line is a second horizontal line, extending from or behind the middle of the upper jaw. Below the second line, there are two or more (usually three) horizontal lines. Often the fourth line branches ventrally from the third line. In the longitudinal pattern, the papillae are elongated perpendicular to the axis of the line only on the second or third and the lowermost (usually the fifth) lines. In all other rows, the papillae are elongated along the axis of the line.

No attempt is made here to standardize the various systems of labelling the papilla lines. Since lines in similar positions in different genera may not always be homologous, a standard system may not be desirable. The labelling used here refers only to the papilla lines under the eye and on the cheek and preoperculum, and is designed to distinguish the orientation of the papillae within the lines. The first letter refers to the orientation of the line: V = more or less vertical; L = longitudinal, or more or less horizontal. The second letter indicates the orientation of the papillae with respect to the axis of the line: T = transverse or perpendicular; A = axial, along the axis of the line. VT1, VT2, etc. = vertical papilla lines with papillae oriented at right angles to the long axis of the line. The numbering system begins at the anteriormost vertical line below the eye. LA1, LA2, etc. = longitudinal papilla lines with the papillae oriented along the axis of the line. The numbering system begins with the first line below the eye. VA1 = a vertical row with papillae oriented along the axis of the row, generally present below the front of the eye. LTU = the uppermost longitudinal line with papillae oriented at right angles to the axis of the line. LTB = the lowermost longitudinal line with papillae oriented at right angles to the line. The abbreviations LTU and LTB, referring to upper and bottom horizontal lines respectively are used here in preference to numbers since

these two lines are almost always present in gobioid fishes and are probably homologous.

For the discussion that follows the transverse pattern is defined as the presence of distinct vertical transverse lines (VT) with no apparent longitudinal axial lines. The longitudinal pattern is defined as containing no vertical transverse lines, but only longitudinal axial lines (LA). The longitudinal transverse lines (LTU and LTB) are generally present in both patterns.

Papilla Patterns in *Acentrogobius*

As recognized by Koumans (1953), *Acentrogobius* is clearly a polyphyletic assemblage serving as a convenient dumping ground for problematic species. Hoese & Winterbottom (1979) separated from *Acentrogobius* several coral reef species into the genera *Exyrias*, *Macrodontogobius*, and *Istigobius*, and some estuarine and coastal species into *Favonigobius*, *Amoya*, *Yongeichthys* and *Drombus*.

Because of the confusion over the generic placement of various species, the genus is considered to include for the purposes of this discussion *Acentrogobius viridipunctatus* (Valenciennes) (the type species), *A. therenzieni* Kiener, *A. janthinopterus* (Bleeker), *A. caninus* (Valenciennes), and *A. sp.* However, it is apparent that the genus includes several additional species, most of which have a papilla pattern similar to that of *A. janthinopterus*.

Acentrogobius is distinctive in having a rounded tongue tip, typically a narrow gill opening, extending to just below the pectoral base (except in *A. viridipunctatus*, in which the gill opening extends to below the posterior preopercular margin), no flattened preopercular process at the angle of the preoperculum, no preopercular process connecting to the upper part of the symplectic, and 10 + 16 vertebrae.

A transverse papilla pattern is found in *Acentrogobius viridipunctatus* (Fig. 1) and *A. therenzieni*. The uppermost longitudinal line (LTU)

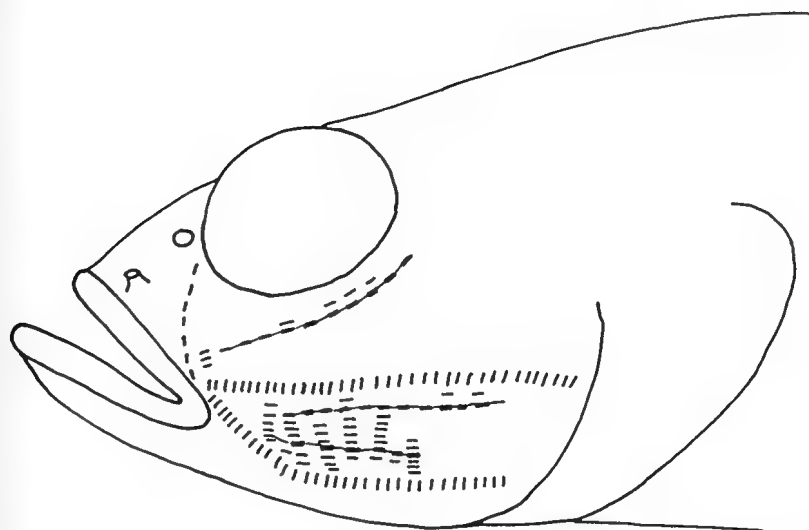


Fig. 4. Sensory papilla pattern in juvenile *Acentrogobius viridipunctatus*, 34 mm SL.

extends from the upper jaw to the end of the preoperculum. There are 5 to 15 short vertical lines (VT) immediately below the eye, few of which reach to the LTU line. Between the two longitudinal lines there are 8 to 16 vertical lines (VT).

A longitudinal pattern is found in *Acentrogobius janthinopterus* (Fig. 2) and *A. caninus*. The two longitudinal lines (LTU and LTB) are essentially identical in position and length to these lines in *A. viridipunctatus*. There are three longitudinal axial lines (LA), the first (LA1) below the eye (reaching the jaws in large adults only), and the other two (LA2 and LA3) between the two longitudinal transverse lines (LTU and LTB).

A mixed pattern is found in *Acentrogobius* sp. (Fig. 3). The longitudinal transverse lines are both reduced in length posteriorly. The second longitudinal axial line (LA2) is well developed, but LA1 and LA3 are reduced in length. There are two vertical transverse lines below the eye and two short VT lines cutting across LA2. The occurrence of this mixed pattern suggests that the two patterns may not be as different as previously thought.

Examination of the longitudinal axial lines in *Acentrogobius janthinopterus* in glycerine-cleared specimens indicates that the papillae in the longitudinal axial lines are connected by a low ridge of skin. These low ridges should not be confused with the large folds or flaps that occur on the cheek in some genera such as *Gobiopsis* (with a longitudinal pattern) and *Callogobius* (with a transverse pattern). The same ridges as found in *A. janthinopterus* are present in *A. viridipunctatus*, suggesting that the transverse pattern in *A. viridipunctatus* was derived from a longitudinal pattern. Supporting evidence for this hypothesis is provided by the pattern of development of the lines with growth in *A. viridipunctatus*. In juveniles (Fig. 4) of *A. viridipunctatus* the longitudinal pattern is readily discernible, although some vertical lines have developed. With growth, the transverse pattern develops more completely. Counts of the number of vertical lines (VT)

and papilla counts in the upper longitudinal transverse lines (LTU) and in the vertical lines, indicates that both the number of lines and the number of papillae in each line increase significantly with growth ($p < .01$, tested with Kendall tau correlation coefficient). The number of vertical lines increases from 5–10 (32–43 mm standard length) to 12–18 (48–83 mm SL).

Ridges connecting the papillae of the longitudinal axial lines also occur in *Acentrogobius* sp.

Consequently, it is suggested that the transverse papilla pattern of *Acentrogobius viridipunctatus* and the mixed pattern of *A. sp.* have evolved from a longitudinal pattern similar to that found in *A. janthinopterus*.

Papilla Patterns in *Glossogobius*

A similar, but somewhat different situation is seen in *Glossogobius*. Of the 12 species of *Glossogobius* illustrated by Akihito & Meguro (1975), only *G. circumspectus* has a transverse papilla pattern. In some species one or more of the longitudinal axial lines may be composed of multiple rows of papillae.

The discussion of *Glossogobius* applies here to the species treated by Akihito & Meguro (1975, 1976), with the exception of *G. biocellatus*. Also included here in *Glossogobius* are *G. tenuiformis* Fowler, from east Africa, *G. bicirrhosus* (Weber) (= *Illana bicirrhosa*), and about 10 to 12 undescribed species from Australia and New Guinea, currently under study by the author and G. Allen.

Glossogobius is highly distinctive in having a bilobed tongue, moderate gill opening extending to under the posterior preopercular margin, no dorsal skin flap at the end of the lower jaw, a flattened bony preopercular process at the angle of the preoperculum (covered by skin), a preopercular extension meeting the symplectic dorsally, and 27 to 29 vertebrae. *G. biocellatus* has a broader gill opening with the gill membranes forming a free fold across the isthmus, no projection at the angle

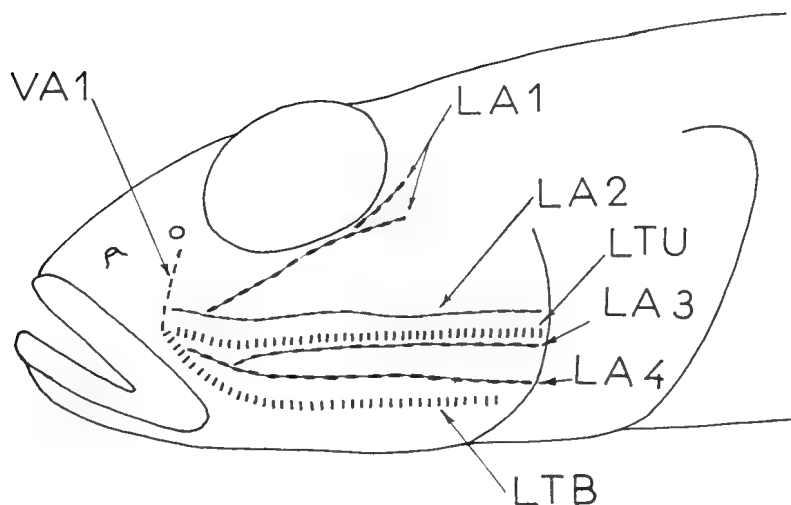


Fig. 5. Longitudinal sensory papilla pattern of *Glossogobius celebius*, 50 mm SL.

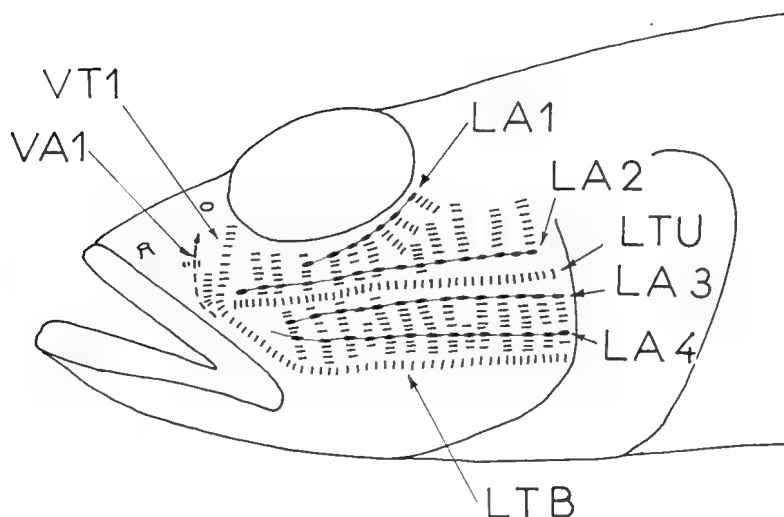


Fig. 6. Transverse sensory papilla pattern of *Glossogobius circumspectus*, 49 mm SL.

of the preoperculum, and a different papilla pattern, suggesting a closer relationship with *Psammogobius* from South Africa. With the exception of *G. bicirrhosus* and *G. circumspectus*, all species are essentially freshwater, only rarely found in brackish water, although the distribution of the larval stages is unknown.

The horizontal pattern characteristic of most species of *Glossogobius* is illustrated in Fig. 5. The short branch of the uppermost longitudinal axial line below the eye is characteristic of only some species of *Glossogobius*. The pattern is similar to the longitudinal pattern of *Acentrogobius*, except there is an additional longitudinal axial line (LA2) just above the upper longitudinal transverse line (LTU). As in *Acentrogobius* all the longitudinal axial lines have a low ridge connecting the papillae within each line. There is a single vertical axial line (VA1) in front of the eye as in *Acentrogobius*. The longitudinal transverse lines (LTU and LTB) extend from the jaws to near the end of the preoperculum, as in most species of *Acentrogobius*.

Glossogobius circumspectus has a distinctive transverse pattern, similar to that of *Acentrogobius*

viridipunctatus, except that the vertical lines above the upper longitudinal transverse line (LTU) are more extensively developed (Fig. 6). Unlike *A. viridipunctatus*, the juveniles (25 to 30 mm SL) of *G. circumspectus* also have a distinctive transverse pattern. Counts of the number of vertical lines and the papillae in the LTU line indicate an increase in the number of lines and papillae with growth ($p < .01$). The number of vertical lines between LTU and LTB increases from 11–14 (30–49 mm SL) to 16–23 (79–108 mm SL). The longitudinal ridges are developed in the same positions as the longitudinal lines (LA1–4) of *G. celebius*, indicating that the transverse pattern in *G. circumspectus* has also developed from a longitudinal pattern.

In *Glossogobius* sp. 16 from Papua New Guinea (Fig. 7) all the axial lines are composed of multiple rows. Although this pattern may represent a transitional stage between the longitudinal and transverse patterns, the presence of secondary ridges parallel to the main LA ridges suggests the pattern may be an independent specialization and is best termed a multiple longitudinal pattern.

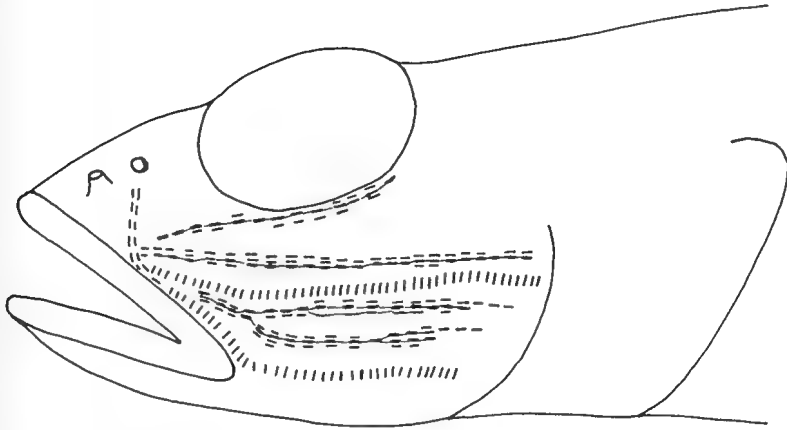


Fig. 7. Multiple longitudinal sensory papilla pattern of *Glossogobius* sp., 50 mm SL.

Discussion

Since *Glossogobius* possesses several specializations not found in *Acentrogobius*, it is suggested that the transverse papilla patterns in these two genera have developed independently from a longitudinal pattern. Although it is possible that the mixed pattern of *Acentrogobius* might be primitive, it is an extremely rare pattern. Even if that pattern is primitive, then both the longitudinal and transverse patterns would have to have developed independently in the two genera, which appears to be the least parsimonious suggestion. Alternatively the transverse pattern could be regarded as primitive, with the longitudinal patterns evolving independently in the two genera. The presence of the longitudinal axial ridges in the transverse patterns in the same position in the respective genera as the longitudinal axial lines does not appear consistent with this hypothesis.

Consequently, it is suggested here that the longitudinal pattern is primitive in *Glossogobius* and *Acentrogobius*, and that the transverse pattern evolved independently in these genera.

It is not clear, however, whether the results obtained here are necessarily broadly applicable to other gobiids. For example, the longitudinal axial ridges are rare in other genera with a transverse pattern. The ridges occur in *Amblygobius* and *Drombus*. The ridges are reduced in *Drombus*, which is probably related to the wider separation of the vertical lines. If the ridges had disappeared in a phylogenetic line, present methods would not be able to distinguish a derived transverse pattern from a primitive one.

Therefore studies of the papilla patterns are useful in characterizing genera, and structural comparisons can aid in determining phylogenies, but it is unlikely that major groupings in a classification can be derived from studies of the papilla patterns.

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Review of the genera of the Barleeidae (Mollusca: Gastropoda: Rissoacea)
..... W.F.PONDER

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Review of the Genera of the Barleeidae (Mollusca: Gastropoda: Rissoacea)

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ABSTRACT. The Barleeidae, a family of minute, marine rissoacean gastropods, is diagnosed and distinguished from the Rissoidae, with which it has usually been associated and with which it is convergent, particularly in shell form. Two subfamilies are recognized, the Barleeinae, containing five genera, two of which are new, and the Anabathrinae, containing 8 genera, one of which is new. The anatomy of several species in both subfamilies is described and the evolution of the female genitalia, in particular, is discussed. The shells, radulae, opercula and, where known, features of the head-foot and anatomy are described for each genus and typical species listed. The Barleeinae is centred in the warm-temperate and tropical eastern Pacific and the Anabathrinae in Australasia. The relationship of the Barleeidae to other families in the lower mesogastropods is briefly discussed.

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The Barleeidae encompasses a compact group of small rissoacean gastropods found mainly in shallow marine habitats in tropical to temperate regions world-wide. They have been included in the Rissoidae by most workers although, since Thiele (1925), *Barleeia* has been regarded as belonging in a separate subfamily. Fretter & Graham (1962) suggested that *Barleeia* might require a separate family on the basis of the anatomical information presented by Fretter & Patil (1961). Nordsieck (1972) and Fretter & Graham (1978) have used Barleeidae as a family, but without adequate discussion. Coan (1964) and Ponder (1967) used both Barleeinae and Anabathrinae, the latter group including several genera previously regarded as typical Rissoidae, as subfamilies of the Rissoidae.

Barleoids, as here recognized, are centred in temperate and subtropical Australasia (the subfamily Anabathrinae) and in western North and Central America (subfamily Barleeinae). They frequently occur in very large numbers on algae in the lower littoral and sublittoral but, despite this, little is known of their taxonomy, biology or ecology. Southgate (1982) has provided some biological and ecological data on *Barleeia unifasciata* (Montagu), the European type species of the family. Fretter & Patil (1961) provided some anatomical information about the same species and Ponder (1968) gave an account of the anatomy of three New Zealand species in the Anabathrinae. Lebour (1934) and Fretter & Graham (1962, 1978) gave a description of the egg capsules and the direct development of *Barleeia unifasciata*.

Judging from their protoconch morphology, all Barleeidae have direct development. The lack of a planktotrophic larval life may have contributed to the relatively high diversity in the two centres of speciation. Their assumed poor dispersal capability may account, at least in part, for the relatively small numbers of species found in areas outside these centres.

The Barleeidae do not have a known fossil record before the Eocene but are presumably Mesozoic in origin. Barleoids are not common as fossils, probably because of their preference for hard-bottom, shallow-water habitats.

There have been only four attempts to group genera in a subfamily around *Barleeia* on a world-wide basis: Thiele (1925, 1929), Wenz (1939), Coan (1964) and Ponder (1967). Thiele (1929) included only two genera (*Anabathron* and *Barleeia*, with *Nodulus* as a subgenus of *Barleeia*). Wenz (1939) added several genera which Ponder (1965a, 1965b) later showed to be eatoniellids and cingulopsids. *Anabathron* was given subfamily status by Coan (1964) and the validity of a subfamily based on this genus (but of considerably different

composition from that envisaged by Coan) was supported by evidence given by Ponder (1967). Coan (1964) included 36 genera and subgenera in his Barleeinae but Ponder (1967) reassigned most of these to other families and some to other subfamilies of the Rissoidae, *Nodulus* being the only genus tentatively included in the Barleeinae apart from *Barleeia*.

Slavoshevskaya (1975) proposed a new family, Ansolidae, on the basis of the female reproductive system of *Ansula* (= *Barleeia* herein) *augustata* (Pilsbry). This family name is here regarded as a synonym of Barleeidae (see below).

The Anabathrinae, together with the Barleeinae, form a cohesive grouping which can be regarded as a family. Some of the important characters typifying this family are the pitted protoconch microsculpture, single oviduct gland, and the presence of a chitinous inner shell layer (Ponder & Yoo, 1976, fig. 12c,d) and a penis. Table 1 lists some of the important characters used to distinguish the subfamilies of the Barleeidae and, for comparison, the Rissoidae. Figure 9 outlines the major characters and character states separating the Barleeidae from several rissoacean and littorinacean families. The relationships of the Barleeidae are more fully explored in the Discussion.

Materials and Methods

The Scanning Electron Microscope (SEM) was used to examine shells, radulae and opercula using the methods given by Ponder & Yoo (1976). Anatomical work was carried out by dissection and by the examination of serial sections stained with Mallory's Triple Stain.

The majority of species described in the family have been examined and these are listed in their original names under each genus together with an indication of the status of the material examined. Species that have had their radula and operculum examined are marked under 'Material Examined' with an asterisk. Material examined alive for head-foot details and preserved material examined for anatomical details referred to under the appropriate headings. Shell descriptions are based on a synopsis of the shell features of the genus but, because of limited suitable material, the examination of protoconch microsculpture has been confined to a few species in each group. These are marked with a dagger in the list of material examined.

Abbreviations Used

AIM: Auckland Institute and Museum, New Zealand.

- AMS: Australian Museum, Sydney.
 ANSP: The Academy of Natural Sciences of Philadelphia, USA.
 auct.: *auctorum* (of authors).
 AUG: Auckland University, Geology Department, Palaeontology collection, New Zealand.
 BMNH: British Museum (Natural History), London.
 BPC: University of California, Paleontology collection, Berkeley, USA.
 CAS: California Academy of Sciences, San Francisco, USA.
 HUM: Museum für Naturkunde, Humboldt-Universität, E. Berlin, DDR.
 LACM: Los Angeles County Museum of Natural History, USA.
 MCZ: Museum of Comparative Zoology, Harvard University, Cambridge, Mass., USA.
 MS: manuscript.
 NHMB: Institut Royal des Sciences Naturelles de Belgique, Brussels.
 NHMV: Naturhistorisches Museum, Wien, Austria.
 NM: Natal Museum, Pietermaritzburg, Natal, South Africa.
 NMNZ: National Museum of New Zealand, Wellington.
 NMV: National Museum of Victoria, Melbourne.
 NMW: National Museum of Wales, Cardiff, UK.
 OUM: The University Museum, Oxford, UK.
 RSM: Royal Scottish Museum, Edinburgh, UK.
 SAM: The South Australian Museum, Adelaide.
 TGM: Instituto di Geologia, Paleontologia e Geografia Fisica, Università di Torino, Italy.
 TM: Tasmanian Museum, Hobart.
 USNM: National Museum of Natural History, Washington, DC, USA.

Taxonomy

Family BARLEEIDAE Gray, 1857

(*ex Barleeiadae* Gray, 1857)

Diagnosis. *Shell:* Small to minute (less than 5 mm in length), broadly-ovate to elongately-conical, umbilicate or non-umbilicate, solid, with inner chitinous layer, smooth or variously sculptured. Aperture with or without varix, rounded to weakly channelled anteriorly and posteriorly. Protoconch paucispiral, dome-shaped, microsculpture of minute pits. Periostracum thin.

Head-foot: Snout short, bilobed; cephalic tentacles long and tapering to short and paddle-shaped, conspicuously or inconspicuously ciliated, eyes in bulges at their outer bases. Pallial tentacles and metapodial tentacles typically absent (posterior pallial tentacle and short, triangular metapodial tentacle present in one genus). Foot short, simple, with or without posterior mucous gland opening by a longitudinal slit reaching to posterior end of foot. Anterior mucous gland present.

Anatomy: Pallial cavity with ctenidium about half the length of, to nearly equal in length to osphradium, ctenidial filaments finger-shaped, their bases narrower than osphradium. Jaws present or absent, odontophore well developed; salivary glands simple, tubular, not passing through nerve ring. Oesophagus lacking oesophageal gland; oesophageal pouches present in some Barleeinae. Stomach with style sac containing crystalline style. Male with penis attached to midline of head behind eyes, or behind right eye; with or without penial prostatic tissue; prostate gland pallial or partly visceral, usually well-developed, closed in most species. Seminal vesicle coiled over inner (ventral) side of stomach. Female with monaulic or diallic genital duct; if diallic, spermathecal opening at posterior end of pallial cavity. Capsule gland well-developed, pallial; albumen gland continuous with capsule gland and embedded in kidney. Ventral channel thin-walled, with sperm channel on left or with separated sperm duct which opens at common aperture with capsule gland at small anterior vestibule, or, in diallic species, absent. Bursa copulatrix, if present, lying on left side of glandular oviduct. Seminal receptacle typically on left side of albumen gland, lying horizontally (i.e. latero-ventrally) and opening near or at junction of upper oviduct with oviduct gland. Upper oviduct simple, narrow. Nervous system with circumoesophageal ganglia concentrated; pedal ganglia abutting against cerebro-pedal ganglia. Renal organ with or without nephridial gland.

Operculum: Oval, pseudoconcentric or concentric with eccentric nucleus, corneous, with or without 1-2 internal pegs or internal ridge.

Radula: Taenioglossate, with few to numerous cusps on teeth. Central teeth with one pair of small basal denticles, lateral margins usually thickened, lateral teeth with short cutting edge (approximately $\frac{1}{2}$ - $\frac{1}{3}$ length of tooth).

Remarks. The Barleeidae is convergent with the Rissoidae, the Eatoniellidae and the Cingulopsidae. The major characters separating the Rissoidae and Barleeidae are listed in Table 1. The opercular characters (pseudoconcentric with a peg in the Barleeinae, double-layered in the Anabathrinae), the inner chitinous shell layer and pitted protoconch microsculpture are all diagnostic of the Barleeidae. This family differs from the Eatoniellidae (Ponder, 1965a, Ponder & Yoo, 1978) in having a penis as well as in many other characters. Species of the Cingulopsidae (Ponder, 1965c, Ponder & Yoo, 1980) also lack a penis and those of the Cingulopsidae and Eatoniellidae lack punctate protoconch microsculpture, have readily distinguishable radulae and differ anatomically. A more detailed discussion of the relationships of the family is given below, and summarized in Fig. 9.

Recognized Genera and Subgenera

The 13 barleeid genera listed below are arranged in the order in which they appear in the text.

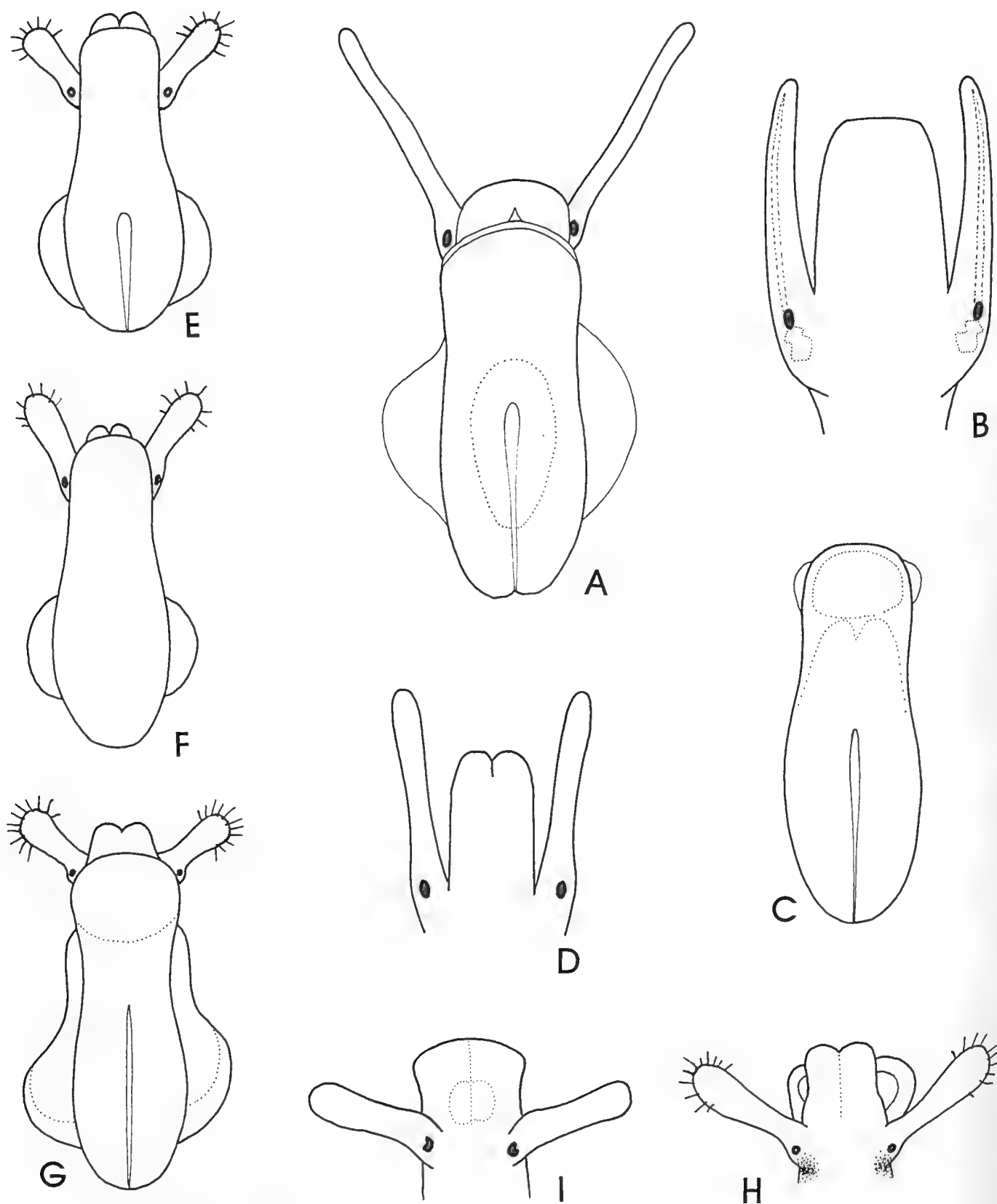


Fig. 1. A & B, Head-foot of *Barleeia unifasciata* (Montagu); Wembury, England. A, ventral view of head and foot; B, dorsal view of head. C & D, Head-foot of *Protobarleeia myersi* (Ladd); Heron Island, Queensland. C, ventral view of foot; D, dorsal view of head. E, Ventral view of head-foot of *Anabathron (Anabathron) contabulatum* (Frauenfeld); Boat Harbour, Cronulla, New South Wales. F, Ventral view of head-foot of *Anabathron (Scrobs) luteofuscus* (May); Boat Harbour, Cronulla, NSW. G & H, Head-foot of *Amphithalamus (Amphithalamus) vallei* Aguayo & Jaume; Missouri Key, Florida, USA G, ventral view; H, dorsal view. I, Dorsal view of head of *Badepigrus pupoides* (Adams); Port Hacking, NSW.

BARLEEINAE

Barleeia
Protobarleeia n.gen.
Lirobarleeia n.gen.
Caelatura
Fictonoba

ANABATHRINAE

Anabathron
Anabathron s.s.
Scrobs
Amphithalamus
Amphithalamus s.s.
Notoscrobs
Microdryas
Badepigrus
Afriscrobs n.gen.
Pseudestea
Pisinna
Nodulus

Key to Subfamilies of Barleeidae

1. Operculum with convex outer surface, composed of one layer and with prominent peg and longitudinal ridge on middle part of inner surface BARLEEINAE
- Operculum with flat surface, composed of 2 layers, with or without peg(s); without longitudinal ridge on middle part of inner surface (a ridge may occur along inner [or columellar] edge) ANABATHRINAE

Subfamily BARLEEINAE

Synonym: ANSOLIDAE Slavoshevskaya, 1975.

Diagnosis. *Shell:* Small to minute (1–5 mm in length), conical, ovate or elongately ovate to elongately conical, non-umbilicate to narrowly umbilicate, solid, with inner chitinous layer moderately to poorly developed, smooth or with axial or spiral sculpture or both. Aperture with simple peristome, with or without varix, angled posteriorly, angled to convex anteriorly, outer lip prosocline to opisthocline. Protoconch dome-shaped, minutely pitted.

Head-foot: With slender, non-tapering to only slightly tapering cephalic tentacles. Foot usually rather short and broad, with or without posterior mucous gland opening by way of long slit in metapodium. Anterior mucous gland well developed. Metapodial tentacle and posterior (right) pallial tentacle present in one genus.

Anatomy: Penis attached behind right eye, externally and/or internally glandular, large, straight. Prostrate gland enclosed in penis or wholly within right pallial wall, or partly protruding into renal organ; closed or (rarely) open. Female pallial duct (of *Barleeia*) with posterior spermatheca separate from distal oviduct opening and capsule gland with thick ventral wall, or

single distal opening and capsule gland with thin ventral wall. Bursa copulatrix present or absent. Oesophageal pouches present in some genera; dorsal folds in mid-oesophagus short.

Operculum: Composed of one layer; oval, yellow or red, outer surface convex, pseudo-concentric, with heavy, internal, longitudinal ridge and prominent peg lying at right angles to longitudinal axis.

Radula: Central teeth with few cusps, lateral margins at 20°–45°, cutting edge triangular; face of tooth with U-shaped ventral projection (absent in one genus) which lies immediately above next tooth (Fig. 17G:p) and, below this, ventral margin (Fig. 17G:m) projects beneath tooth in front. Lateral teeth with few cusps, cutting edge short relative to total length of tooth. Marginal teeth with several cusps on distal ¼–½ of outer edge of inner marginal teeth and inner and/or outer edge of outer marginal teeth.

Remarks. The members of this small subfamily form a compact group distinguished by their peculiar operculum and pitted protoconch.

Slavoshevskaya (1975) proposed a new genus (*Ansola*) and family for *Assimineia angustata* Pilsbry on the basis of the structure of the reproductive system. From the initial brief account and a later (1976) detailed study, there appear to be very few differences between *A. angustata* and *Barleeia unifasciata*. The main difference appears to be in the presence of a pallial prostrate in *B. unifasciata* whereas in *A. angustata* the prostatic tissue is contained in the penis. As all other aspects of the morphology of *A. angustata* and *B. unifasciata*, including their shell, opercular and radular features, appear to be very similar I regard *Ansola* as a synonym of *Barleeia*.

The species of Barleeinae are centred along the west coast of North and Central America including the Galapagos Islands. A few are found in most other temperate and tropical seas; mainly in shallow water.

General Anatomical Account of the Barleeinae

This description of the anatomy of the Barleeinae is based on five species of *Barleeia*: *B. acuta* (Carpenter) and *B. haliotiphila* (Carpenter) from Monterey, California, U.S.A., *B. unifasciata* (Montagu) from Bantry Bay, SW Ireland, *B. cf. tincta* (Guppy) from Fort Pierce, Florida, U.S.A., and *B. angustata* (Pilsbry) (the last based on data from Slavoshevskaya, 1975, 1976), *Lirobarleeia galapagensis* (Bartsch), from Academy Bay, Santa Cruz Island, Galapagos Islands, and *Fictonoba carnosus* (Webster) from Takapuna, Auckland, New Zealand.

The pallial cavity. The pallial cavity contains a well-developed, elongately oval osphradium with a central sensory area which contains the osphradial ganglion. The osphradium is surrounded by a border-like ciliated ridge on both sides. The ctenidium is longer than the osphradium (which varies from a little over half the length of the ctenidium to only slightly shorter), and is composed of well-developed, finger-shaped filaments.

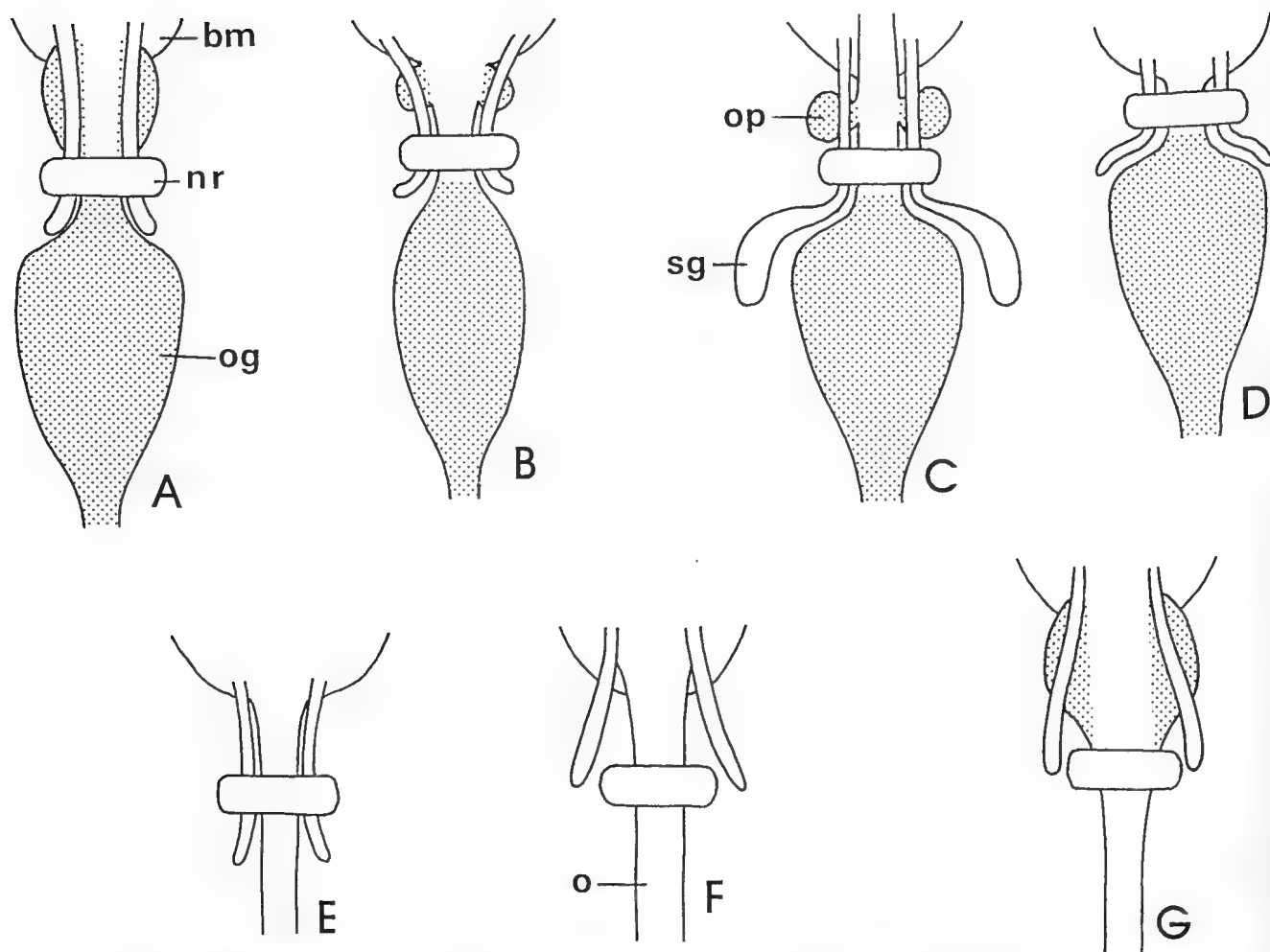


Fig. 2. Diagrammatic representations of the mid-oesophagus of selected rissoid and littorinid species to show the relationships of the salivary glands and oesophageal gland to the nerve ring. For further explanation see 'Discussion'. A, *Eatoniella* spp. (Eatoniellidae) and *Macquariella kingensis* (May) (Littorinidae). B, *Laevilitorina mariae* (T. Woods) (Littorinidae). C, *Littorina* spp. (Littorinidae). D, *Eatonina rubrilabiata* Ponder & Yoo (Cingulopsidae). E, *Skenella castanea* (Laseron) (Cingulopsidae). F, Rissoidae and Anabathrinae. G, *Barleeia* spp. (Barleeinae).

bm, buccal mass; nr, nerve ring; o, oesophagus; og, oesophageal gland; op, oesophageal pouch; sg, salivary gland.

A hypobranchial gland is present but is not thickly developed. In *Fictonoba carnosa* the posterior part of the gland is dark brown.

The pedal glands. The foot contains an anterior pedal gland which consists of a core of glandular tissue reaching to the base of the cephalic haemocoel to lie beneath the buccal mass. *Lirobarleeia galapagensis* and species of *Barleeia* also have a posterior pedal gland that opens, in *Barleeia*, into a long midventral slit. No species of *Lirobarleeia* have been observed alive but they probably have a similar slit. *Fictonoba carnosa* lacks the posterior pedal gland but has a similar anterior pedal gland.

The digestive system. There is a well-developed buccal mass with a powerful odontophore. The oral tube does not contain any jaws in *B. angustata* and *B. unifasciata* but a rudimentary jaw is present in *B. haliotiphila*. This is composed of a pair of dark-staining patches of chitin projecting slightly from the oral tube.

In *B. acuta* and *B. cf. tincta* a pair of small jaws is present consisting of short rodlets. *Fictonoba carnosa* and *Lirobarleeia galapagensis* lack jaws.

The anterior oesophagus opens to the buccal cavity and in the species of *Barleeia* and in *Lirobarleeia galapagensis* is surrounded by a pair of sac-like extensions of the oesophagus. These lie anterior to the nerve ring and are probably homologous with the oesophageal pouches of the Littorinidae. The pouches open laterally to the oesophagus (Fig. 2G) and contain an epithelium similar to that of the oesophageal gland of lower mesogastropods (see 'Discussion' for further comment on the homology of these structures). The anterior oesophagus in *Fictonoba carnosa* is simple, having no trace of similar structures. The dorsal folds in the anterior oesophagus are short in the three genera examined and do not persist behind the nerve ring.

The tubular salivary glands are simple and extend back to the nerve ring and lie dorsal to it. There are two

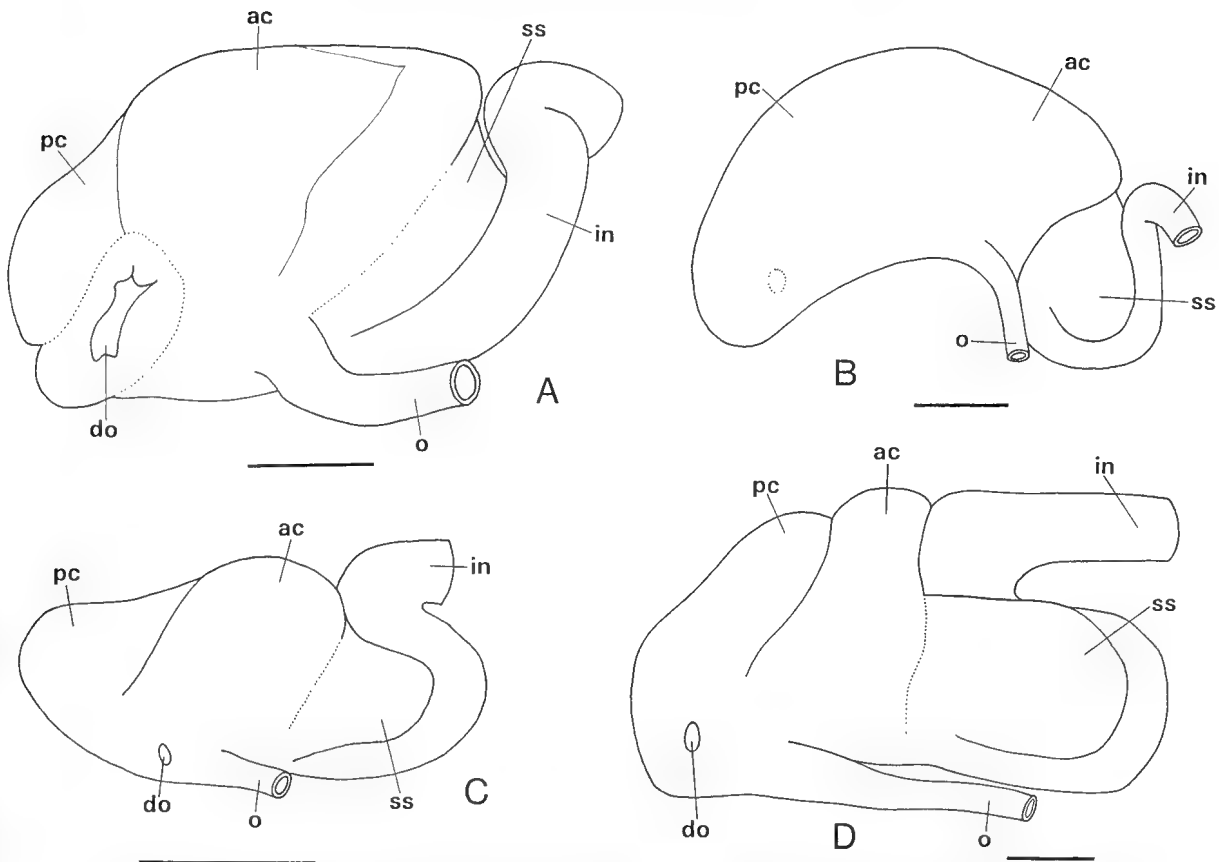


Fig. 3. Stomachs of some species of Barleeidae. A, *Barleeia acuta* (Carpenter); Monterey Peninsula, California, USA. B, *Fictonoba carnosa* (Webster); Takapuna, Auckland, New Zealand. C, *Amphithalamus incidatus* (Frauenfeld); Boat Harbour, Cronulla, NSW. D, *Pisinna frauenfeldi* (Frauenfeld). Boat Harbour, Cronulla, NSW. ac, anterior chamber; do, digestive gland opening; in, intestine; o, oesophagus; pc, posterior chamber; ss, style sac. Scale: 0.2 mm

types of secretory cell present in all three genera. The simple, narrow posterior oesophagus opens to the spacious stomach (Fig. 3A,B) which is of the usual structure for a microphagous mesogastropod. The stomach has a style sac which contains a crystalline style. The style sac (Fig. 3: ss) is short relative to the rest of the stomach in the three genera examined but the stomach is relatively shorter in *Barleeia* (Fig. 3A) than in *Fictonoba* (Fig. 3B) or *Lirobarleeia*. The intestine loops around the style sac towards the outer end of the anterior chamber and then follows a rather straight course along the right pallial wall to a little behind the outer edge of the pallial cavity.

The digestive gland opens to the stomach just behind the oesophageal opening by way of a single opening (Fig. 3: do). The excretory cells contain vacuoles with dark brown spherules in *Barleeia* species, although these are less abundant than in many rissoaceans. What appear to be the same vacuoles in *Fictonoba carnosa* are filled with several tiny refringent yellowish granules and lack spherules. The material of *L. galapagensis* was not fixed adequately to determine whether or not spherules were present.

The renal organ. The simple, sac-like renal organ is situated immediately behind the posterior pallial wall, through which it opens by way of a small aperture. There is a thick, glandular pad (nephridial gland) on the outer wall.

The nervous system. This has been studied only for *Barleeia acuta*, *B. angustata* (by Slavoshevskaya, 1976) and *Fictonoba carnosa*. The cerebral ganglia are separated by a short commissure, the pleural ganglia are fused to the cerebral ganglia and the pedal ganglia are fused to the cerebro-pleurals (in *Barleeia*), but are joined by short connectives in *F. carnosa*. The supraoesophageal connective is about two-thirds the length of the supraoesophageal ganglia in *F. carnosa*, but in the two species of *Barleeia* the ganglia almost abut. The suboesophageal connective is indistinguishable in *Barleeia* spp. and about one-third the length of the suboesophageal ganglion in *F. carnosa*. The pedal ganglia are about the same size as the cerebral ganglia in *Barleeia* spp. (information not available for *F. carnosa*).

Slavoshevskaya (1976) gives some additional details about the nervous system of *Barleeia angustata*.

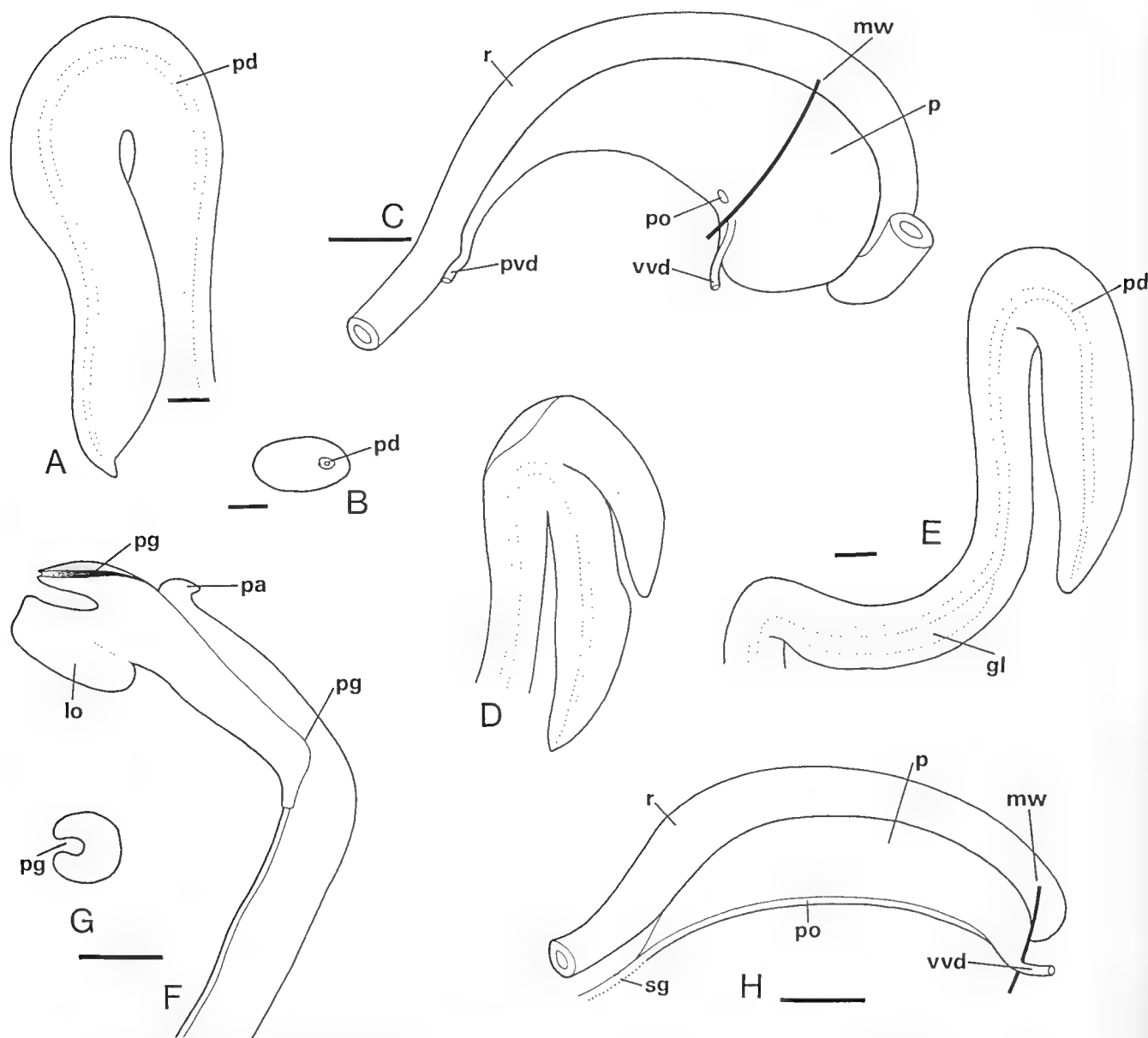


Fig. 4. Male genitalia of Barleeiinae. A-C, *Barleeia acuta* (Carpenter), Monterey Peninsula, California, USA. A, dorsal view of penis at rest (preserved specimen); B, transverse section of penis (semi-diagrammatic); C, prostate gland and part of the intestine-rectum. D & E, penis of *Lirobarleeia galapagensis* (Bartsch), Bahia Academy, Isla Santa Cruz, Galapagos Islands. D, distal end of specimen with bifurcate penis; E, specimen with simple penis. F-H, *Fictonoba carnosa* (Webster); Takapuna, Auckland, New Zealand. F, penis from preserved specimen; G, transverse section of shaft of penis (semi-diagrammatic); H, prostate gland and part of the intestine-rectum. gl, internal glandular area; lo, glandular lobe; mw, posterior wall of pallial cavity; p, prostate gland; pa, papilla-like projection; pd, penial duct; pg, penial groove; po, pallial opening to prostate gland; pvd, pallial vas deferens; r, rectum; sg, seminal groove; vvd, visceral vas deferens. Scales: 0.1 mm.

The male reproductive system (Fig. 4). Males of all the species listed above were examined histologically except *Lirobarleeia galapagensis*, in which the gross anatomy of the male reproductive system was examined. The testis is rather indistinctly lobed and lies above the digestive gland over all but about the last whorl of the visceral coil. The visceral vas deferens (Fig. 4: vvd) is expanded to form a seminal vesicle which either lies loosely undulating behind the stomach (in *L.*

galapagensis and *B. acuta*), extends straight over the inside (ventral) wall of the stomach (in *B. cf. tincta*), or is coiled over the inside wall of the posterior end of the stomach (in *Fictonoba carnosa*). The seminal vesicle contains typical (eupyrene) and atypical (? apyrene) sperm in *Barleeia* species (as described in detail by Slavoshevskaya, 1976 for *B. angustata*) but only typical sperm in *Fictonoba carnosa*.

The prostate gland (Fig. 4: p) lies either entirely in

the posterior part of the pallial cavity (as in *B. unifasciata* and *F. carnosa* [Fig. 4H]) or partly embedded in the kidney and partly within the pallial wall (*B. acuta* [Fig. 4C], *B. haliotiphila*, *B. cf. tincta* and *Lirobarleeia galapagensis*), or there is no pallial prostate gland, the pallial vas deferens being a simple, narrow tube (as in *B. angustata*). The prostate gland is open to the pallial cavity by way of a short, narrow, ciliated duct (Fig. 4C: *po*) which arises at the junction of the pallial vas deferens with the prostate gland (at the posterior pallial wall). There appears to be a short slit open to the pallial cavity in the prostate of *Lirobarleeia galapagensis* but this was difficult to ascertain with certainty in the material available. The prostate lumen in both *L. galapagensis* and *Barleeia* spp. is a centrally-placed slit. In *Fictonoba carnosa* (Fig. 4H) the prostate gland is open ventrally in all but the most posterior section. The pallial vas deferens in *F. carnosa* is a ciliated groove (Fig. 4H: *sg*) which emerges from the distal end of the prostate gland. The prostatic tissue contains granules which in *F. carnosa* stain blue and yellowish orange within the same cell but are only blue in *Barleeia* spp. The visceral vas deferens enters the prostate gland immediately behind the posterior pallial wall. The pallial vas deferens leaves immediately in front of this wall in *B. haliotiphila* and at the distal end of the gland in *B. unifasciata* and *Lirobarleeia galapagensis*. The pallial vas deferens lies just beneath the epithelium, is weakly muscular and is ciliated.

The penis in species of *Barleeia* (Fig. 4A,B) is long (longer than the pallial cavity), slender (relative to its length), coated with epithelial gland cells, and usually bent back on itself. In *B. haliotiphila* and *B. acuta*, these cells are modified distally into a clump of glandular columnar cells, the granular contents of which stain purple-red. The penial duct is ciliated, weakly muscular and lined with cuboidal epithelium. In *B. angustata* this epithelium is modified to form prostatic tissue (Slavoshevskaya, 1975, 1976). In *Lirobarleeia galapagensis* (Fig. 4D,E) the penis is also long and rather slender but is expanded distally. Of the three specimens examined one had a discrete flat lobe a little behind the distal end (Fig. 4D), but in the other two specimens the distal end of the penis was simple, flattened and expanded (Fig. 4E). A dense-white, glandular zone (Fig. 4E: *gl*) lies internally alongside the penial duct in the proximal third of the penis in this species and a similar development was evident in sections of *B. acuta*. The penis of *Fictonoba carnosa* (Fig. 4F,G) is similar to that of *Lirobarleeia galapagensis* and *Barleeia* spp. in that it is large relative to the rest of the animal, and is placed behind the right eye. It is, however, more complex in construction and has an open penial groove (*pg*), not a closed duct. The distal portion of the penis has an expanded, flange-like, glandular lobe (*lo*), a narrow distal portion along which the deep penial groove passes and, at the base of this latter part, a smaller, papilla-like projection (*pa*). The glandular lobe contains a mass of purple-red-staining gland cells which lie amongst radial muscle fibres.

The female reproductive system (Figs 5, 6). The ovary is compact, and contains large, yolky eggs in all species. The upper oviduct is narrow and thickens slightly before entering the fertilization area. This short, thickened region, the renal oviduct, is lined with cuboidal to short columnar cells and has a narrow lumen in *Barleeia unifasciata*, *B. acuta*, *B. haliotiphila* and *Fictonoba carnosa*. The nature of the renal oviduct in *Lirobarleeia* was not determined. In *Barleeia angustata* the renal oviduct is lined with columnar cells with irregular apices and basal nuclei which resorb spermatozoa (Slavoshevskaya, 1976). No indication of this phenomenon was observed in any of the species I have examined. The renal oviduct opens to the 'fertilization chamber' in species of *Barleeia* and in *Lirobarleeia galapagensis*, and to the albumen gland in *Fictonoba carnosa*.

The fertilization chamber (Figs 5G, 6: *fc*) in species of *Barleeia* is a ventral sac just behind the posterior end of the capsule gland. It is lined with ciliated cells and goblet cells and opens by way of a short, ciliated spermathecal duct (Fig. 6: *sd*) to the posterior pallial cavity. The renal oviduct (Fig. 5G: *od*) opens to this chamber in a short, muscular papilla (Fig. 6: *p*). The opening is closed by what is assumed to be a sphincter muscle in all the material sectioned. There is a small, posterior, latero-ventral (left) seminal receptacle (Figs 5G, 6: *sr*) which opens to the fertilization chamber. The fertilization chamber lies below the large albumen gland (Figs 5G, 6: *ag*), which opens to the chamber. This gland is continuous with the capsule gland (Figs 5G, 6: *cg*) and the capsule gland does not open independently to the fertilization chamber. The albumen gland extends anteriorly as a long lobe reaching into the pallial wall to lie above the posterior end of the capsule gland. This anterior lobe (Figs 5G, 6: *ss*) is considerably thinner-walled than the rest of the albumen gland and is lined with pale blue-staining, glandular, short columnar cells with wedge-shaped ciliated cells between. The histology is essentially similar to that of the albumen gland except that the gland cells of that structure are much longer and contain much larger granules which stain dark blue. The lobe contains spermatozoa (Figs 5G, 6: *sz*) which have their heads attached to the epithelium. This structure is referred to as a seminal receptacle in *B. angustata* by Slavoshevskaya (1976), and the structure here referred to as the seminal receptacle was identified as the bursa copulatrix by that author. Although this modified part of the albumen gland was identified in *B. unifasciata*, the rather poor sections available of that species did not show any sperm present.

The capsule gland in species of *Barleeia* is oval in section (Fig. 5H) with a slit-like lumen with glandular epithelium ventral (and dorsal) to the ends of the lumen. The distal opening (Fig. 5G: *ga*) is simple and by way of a narrow, ciliated vestibule.

Lirobarleeia galapagensis has a female reproductive system which is generally similar to that of species of *Barleeia* but differs in several important respects. A seminal receptacle (Fig. 5C: *sr*) is present and opens to

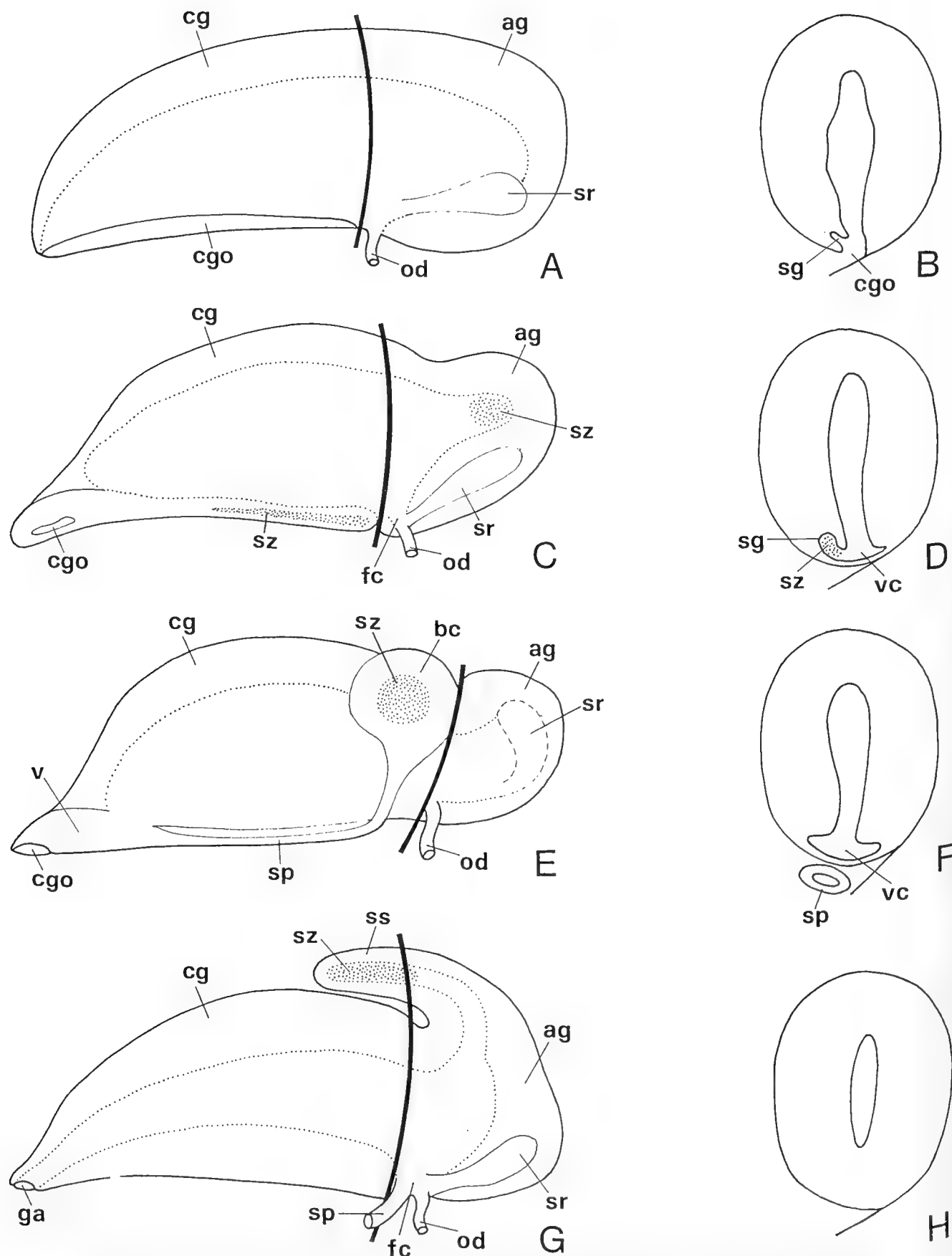


Fig. 5. Semidiagrammatic representations of the female genital systems of some Barleeinae, as seen from the left (inner) side with a section through the middle region of the capsule gland. A & B, hypothetical ancestor. C & D, *Lirobarleeia galapagensis* (Bartsch). E & F, *Fictonoba carnosa* (Webster). G & H, *Barleeia* spp. ag, albumen gland; bc, bursa copulatrix; cg, capsule gland; cgo, common genital opening; fc, fertilization chamber; ga, oviducal opening; od, upper oviduct; sg, sperm groove; sp, spermathecal tube; sr, seminal receptacle; ss, sperm storage area; sz, spermatozoa; v, vestibule; vc, ventral channel.

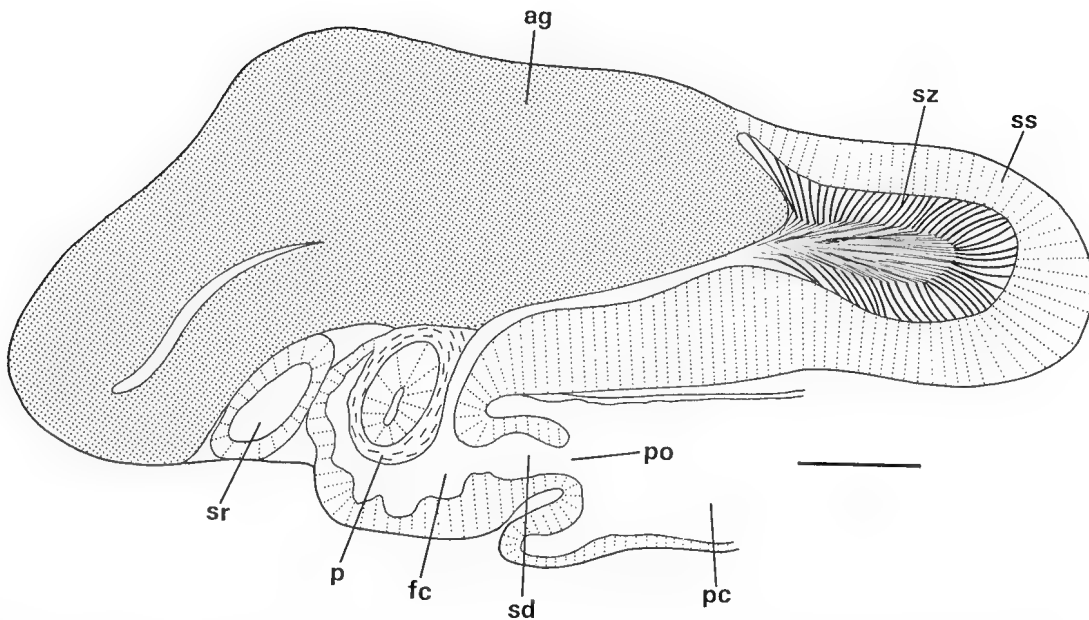


Fig. 6. Longitudinal section of part of the female genital system of *Barleeia haliotiphila* (Carpenter). The figure shows the spermathecal opening to the pallial cavity and the sperm sac derived from the modified albumen gland. ag, albumen gland; fc, fertilization chamber; p, papilla; pc, pallial cavity; po, pallial spermathecal opening; sd, spermathecal duct; sr, seminal receptacle; ss, sperm sac; sz, spermatozoa. Scales: 0.05 mm.

a fertilization chamber along with the renal oviduct (Fig. 5C: *od*), which does not appear to be produced into a muscular papilla. The fertilization chamber (Fig. 5C: *fc*) lies beneath the albumen gland (*ag*) and opens to this gland just behind the capsule gland (*cg*). The albumen gland appears to be folded into at least a U-shaped fold in sections but the details could not be determined in dissection. The albumen gland is partly divided off from the capsule gland although it is continuous with it. There is no dorsal, forwardly-projecting lobe modified for sperm storage but the albumen gland does appear to store small quantities of sperm. The poor fixation of the material, however, did not allow this to be established with certainty. The capsule gland has a thin-walled ventral channel (Fig. 5D: *vc*) which contains a well-developed sperm groove (*sg*) separated from the lumen of the gland by a longitudinal, non-muscular fold on the left side. This groove contains a mass of sperm (Figs 5C,D: *sz*) and appears to terminate blindly at the posterior end of the capsule gland. At this point the rest of the ventral channel (i.e. that part not the sperm groove) opens to a small, thin-walled, ventral sac (= the fertilization chamber) (Fig. 5C: *fc*). Anteriorly the sperm groove closes over just before reaching the vestibule to form a separate duct

and then opens within the narrow vestibule/vagina, although the sperm groove and oviduct remain separated by a dorsally-attached, longitudinal flap of tissue right to the terminal opening (*cgo*).

The fertilization chamber in *Fictonoba carnosa* is a thin-walled section of the antero-ventral part of the albumen gland into which the seminal receptacle (Fig. 5E: *sr*) and renal oviduct (*od*) open. The seminal receptacle lies on the right side of the albumen gland, is lined with a pavement epithelium and contains semi-orientated sperm. The renal oviduct opens at a small papilla-like structure, smaller and less muscular than in *Barleeia*. The albumen gland (*ag*) and capsule gland (*cg*) are separate lobes but continuous ventrally. A thin-walled ventral channel (Fig. 5F: *vc*) in the capsule gland does not contain a sperm groove, but instead a separate spermathecal tube (*sp*) lies ventrally to it. This tube opens anteriorly into a large ciliated vestibule (Fig. 5E: *v*) which is apparently not used for sperm storage. The spermathecal tube passes dorsally on the left side of the posterior end of the capsule gland to open to a latero-dorsal bursa copulatrix (Fig. 5E: *bc*). This structure is lined with columnar cells with irregular apices and was empty of sperm in most of the specimens sectioned.

Key to the Genera of the Barleeinae

1. Shell ovate-conic to conic, smooth or with spiral sculpture 2
- Shell elongate-conic to elongate-pupoid, smooth or with spiral and/or axial sculpture 3

2. Shell smooth or with weak spiral striae; protoconch microsculpture of regular, spirally-arranged pits *Barleeia*
 — Shell with spiral cords; protoconch microsculpture of spiral ridges and honey-comb-like pits *Protobarleeia* n.gen.
3. Teleoconch with microsculpture of minute pits; axial or spiral sculpture, or smooth *Caelatura*
 — Teleoconch without microsculpture of minute pits; axial and/or spiral sculpture, rarely smooth 4
4. Protoconch microsculpture of irregular, shallow pits; penis with open seminal groove *Fictionoba*
 — Protoconch microsculpture of irregular, deep pits; penis with closed duct *Lirobarleeia* n.gen.

Genus *Barleeia* Clark, 1853

Barleeia Clark, 1853: 292. Type species *Turbo ruber* J. Adams, 1797, not von Salis, 1793 (= *T. unifasciatus* Montagu, 1803); by monotypy. Recent, eastern Atlantic and Mediterranean Sea. (Figs 1A,B; 10 A-E).

Barleia, *Barleeja* err. auct.

Pseudodiala Ponder, 1967: 219. Type-species *Diala acuta* Carpenter, 1864; by original designation. Recent, western North America (Figs 3A, 4A-C; 11 A-D)

Ansola Slavoshevskaya, 1975: 119. Type-species *Assimineia angustata* Pilsbry, 1901; by original designation. Recent, north-western Pacific (Fig. 10F,G).

Diagnosis. *Shell:* Small (1–4 mm), rather solid, conic to ovate-conic, non-umbilicate, smooth or with weak spiral threads, periphery convex to angled. Aperture with simple peristome, angled but not channelled posteriorly, subangled to rounded anteriorly. Outer lip usually prosocline, rarely orthocline or opisthocline, with or without varix, thin, with sharp edge (Figs 10A,F; 11A). Protoconch paucispiral, dome-shaped, with numerous small pits arranged more or less in spiral series; sometimes with narrow, unpitted spiral bands, but no raised spiral ridges (Figs 10B, 11B). Inner chitinous layer moderately well developed.

Head-foot: Pigmented; snout broad, rather short, bilobed. Cephalic tentacles long, not noticeably ciliated, eyes in bulges at their outer bases. Foot rather short and broad, anterior and posterior mucous glands present, posterior gland opens into posterior half of sole by longitudinal slit. No metapodial or pallial tentacles (Fretter & Graham, 1962; fig. 289B; Fretter & Graham, 1978; own observations [*B. unifasciata*, Plymouth, England; *B. calcarea* Kay, Diamond Head, Oahu, Hawaiian Islands; *B. cf. tincta*, Fort Lauderdale, Florida; *B. haliotiphila* and *B. acuta*, Monterey, California, U.S.A.]). (Fig. 1A,B.)

Anatomy: Oesophageal pouches present. Penis (Fig. 4A,B) behind right eye, long, tapering to sharp point. Prostate gland pallial + visceral (Fig. 4C) pallial or penial (Slavoshevskaya, 1976, fig.2). Capsule gland with thick ventral wall, spermathecal opening at posterior end of pallial cavity. Albumen gland modified for sperm storage. No bursa copulatrix (Figs 5G, 6). (Based on *B. unifasciata*, *B. cf. tincta*, *B. haliotiphila*,

B. acuta and *B. angustata*; see anatomical account for further details.)

Operculum: Solid, usually red, with strong, internal longitudinal ridge. A long peg emerges from nucleus and extends beyond inner (columellar) edge (Figs 10C,D,G, 11C).

Radula: Central teeth with large, rectangular median cusp, 2–3 small, sharp lateral cusps and a pair of basal denticles; lateral margins narrowly thickened, at about 20°–45°; base with U-shaped projection. Lateral teeth 2 + 1 + 2(–3), median cusp about twice as long as lateral cusps. Marginal teeth with subequal cusps; cusps on outer edge of outer marginal teeth (Figs 10E, 11D).

Egg capsules: Ovoid, with small area of attachment; contain single egg (*B. unifasciata*; Lebour, 1934, Fretter & Graham, 1962, 1978).

Distribution. Western North America (*Barleeia haliotiphila* Carpenter, 1864; *B. subtenius* Carpenter, 1864; *Jeffreysia alderi* Carpenter, 1856; *Cingula paupercula* C.B. Adams, 1852 = *Barleeia zeteki* Strong & Hertlein, 1939; *Jeffreysia bifasciata* Carpenter, 1856; *Diala acuta* = *Diala marmorea* Carpenter, 1864 = *Barleeia dalli* Bartsch, 1920; *Barleeia oldroydi*, *B. sanjuanensis*, *B. bentleyi*, *B. californica*, *B. coronadoensis*, *B. carpenteri*, *B. orcutti*, all Bartsch, 1920). Caribbean (*Barleeia tincta* Guppy, 1895). South-western Atlantic (*Eatoniella rubrooperculata* Castellanos & Fernandez, 1972). Europe and Mediterranean Sea (*T. unifasciatus* = *ruber* J. Adams, 1797, not von Salis, 1793, = *Rissoa fulva* Michaud, 1830 = *Subanea binghamiana* Leach, 1852; *Rissoa seminula* Monterosato, 1877). St. Helena (*Rissoa cala* Smith, 1890, ? = *Rissoa ephamilla* Smith, 1890; *Rissoina congenita* Smith, 1890). East Africa (*Barleeia tropica* Thiele, 1925). South Africa (*Rissoa (Cingula) caffra* Sowerby, 1897 = *Microsetia kraussi* Turton, 1932). Mauritius (*Barleia* [sic] ?*microthyra* Martens, 1880). Japan (*Diala simplex* Smith, 1875; *Barleeia trifasciata* Habe, 1960). South-east Asia (*Cingula annamitica* Dautzenberg & Fischer, 1907). Australia (at least 3 undescribed species). Hawaii (*Barleeia calcarea* Kay, 1979). North Pacific (*A. angustata*). Miocene of Italy (*Barleeia rubra* var. *mioelongata* Sacco, 1895 and

var. *miocenica* Sacco, 1895 appear to be the same taxon).

Barleeia simplex Briart & Cornet, 1887, an Eocene species from Europe, has not been examined. It becomes a secondary homonym of *B. simplex* (Smith, 1875) so a replacement name, *B. eocenica* nom. nov., is provided herein for it.

Material examined.

†**T. unifasciatus*: Many lots (BMNH, AMS, etc).

†**R. seminula*: Author's material (BMNH, AMS).

B. tropica: Syntypes (HUM).

J. caffra: Syntypes (BMNH) and a few other specimens (AMS, ANSP).

R. cala: Syntypes (BMNH, ANSP, NHMB, USNM).

R. ephamilla: Syntypes (BMNH), 1 lot (USNM).

B. congenita: Syntypes (BMNH, ANSP).

†**A. angustata*: Holotype (ANSP) and one other lot ex Golikov (AMS).

M. kraussi: Holotype and paratypes (OUM).

D. simplex: Holotype; has operculum visible in shell (BMNH).

†**B. microthyræ*: Syntypes (HUM, AMS) and a few other lots (AMS).

B. rubra var. *mioelongata* and var. *miocenica*: Types (TGM).

†**B. calcarea*: A few lots (AMS).

B. tinctoria: Syntypes (USNM) and a few other lots (USNM, MCZ, ANSP).

†**D. acuta* and several other west American species, including *B. sanjuanensis** (AMS, LACM) and types of all other species listed have been examined.

†*undescribed Australian species (AMS).

Remarks. There is a considerable range of shape, size and colour in this genus, with many species brightly coloured, some banded and others white.

Pseudodiala was erected as a subgenus of *Barleeia* to include the west American species previously included in *Diala* Adams. The type species differs from other species of *Barleeia* in having a strong peripheral angulation and an opisthocline, varicose outer lip. Although it is a distinctive species, a few others show various degrees of angulation of the periphery. There are no significant radular, opercular or anatomical differences between the type species of *Pseudodiala* and *Barleeia*, so that, in the absence of additional supporting evidence, *Pseudodiala* is here regarded as a synonym of *Barleeia*. *Ansola* is discussed in the 'remarks' on the subfamily.

Species of *Barleeia* typically have smooth shells, although the shell of *B. cala* (Smith) is weakly spirally striate.

Protobarleeia n.gen.

Type species: *Amphithalamus (Cerostraca?) myersi* Ladd, 1966. Late Miocene, Eniwetok Atoll, Pacific Ocean. Also Recent, SW Pacific (Fig. 11E-I).

Diagnosis. *Shell:* Minute (1.5–2 mm in length), solid, ovate-conic, non-umbilicate, with spiral lirae.

Teleoconch microsculpture of fine, dense, rather irregular spiral threads. Aperture oval, very weakly subangled anteriorly and posteriorly (Fig. 11E); outer lip orthocline, with a prominent external varix. Protoconch of about $1\frac{3}{4}$ whorls, sculptured with well-spaced, raised spiral cords, the interspaces with an anastomosing microsculpture giving it an irregularly netted appearance (Fig. 11F).

Head-foot: As in *Barleeia* but unpigmented (Heron Island, Queensland, Australia) (Fig. 1C,D).

Anatomy: Not known.

Operculum: As in *Barleeia*, but yellow (Fig. 11G,H).

Radula: As in *Barleeia*; central teeth $\frac{2}{1} + 1 + \frac{2}{1}$; lateral edges at 30°. Lateral teeth $2 + 1 + 2$ (Fig. 11I).

Distribution. Western Pacific; late Miocene to Recent (*A. myersi* Ladd).

Material examined.

A. myersi: Several lots from Fiji and Queensland, Australia (AMS).

Remarks. This monotypic genus has been created for a peculiar, minute barleeid which differs from the other genera in the subfamily in having spiral sculpture on both protoconch and teleoconch and a yellow operculum. The microsculpture of the protoconch is also quite different from that of *Barleeia* (compare Figs 10B and 11B with 11F).

Ladd (1966) named the type species on the basis of a single specimen from the upper Miocene of Eniwetok. There are in the AMS several lots of this species from localities in Fiji and Australia which agree very closely with Ladd's description and figure.

Lirobarleeia n.gen.

Type species: *Alvania galapagensis* Bartsch, 1911. Recent, Galapagos Islands, eastern Atlantic (Figs 4D,E; 5C,D; 12A–D).

Diagnosis. *Shell:* Small (2–4 mm in length), elongate-conic, solid, non-umbilicate with spiral and axial sculpture, the spiral elements usually predominant, type species clathrate, rarely smooth. Aperture with simple peristome, rounded to weakly angled anteriorly, weakly angled and, in a few species, very weakly channelled, posteriorly. Outer lip weakly opisthocline to orthocline, with varix (Figs 12A,E; 13A; 14A). Protoconch with whole surface very minutely and irregularly pitted, sometimes with weak spiral ridges unrelated to the pitted microsculpture (Fig. 14B, C), or with strong spiral ridges (Figs 12D,F; 13D,E). Inner chitinous layer moderately well developed.

Head-foot: Known only from preserved material of *A. galapagensis*; appears to closely resemble *Barleeia*.

Anatomy: Oesophageal pouches present. Penis (Fig. 4D,E) with broad distal lobe; prostate gland pallial + visceral. Capsule gland with very thin ventral connection between two halves of gland; oviduct opening distal, no separate spermathecal aperture. Albumen gland lacking a modified sperm pouch; no

bursa copulatrix (Fig. 5C,D) (*L. galapagensis*) (see anatomical account for further details).

Operculum: As for *Barleeia* (previously described for *L. kelseyi* [Baker, Hanna & Strong, 1930] and *L. lirata* [Carpenter, 1856]) (Figs 12C; 13B,C; 14D,E).

Radula: As for *Barleeia*; central teeth $\frac{2-3+1+2-3}{1}$, outer lateral cusps very small; lateral angles at 30–40°. Lateral teeth 2–3 + 1 + 2–4. Marginal teeth with several cusps, distal cusps larger than cusps on outer edges, subequal in both teeth (Figs 12B, 13G, 14F).

Distribution. Tropical western North and central America and the Galapagos Islands (*Rissoa albolirata* Carpenter, 1864; *Rissoa kelseyi* Dall & Bartsch, 1902 = *Alaba oldroydi* Dall, 1905 = *Rissoina lapazana* Bartsch, 1915 = *Alvania bartolomensis* Bartsch, 1917 = *Rissoina lowei* Strong, 1938; *Diala electrina* Carpenter, 1864, = *Alvania lucasana* Baker, Hanna & Strong, 1930; *Rissoa lirata* Carpenter, 1856; *Alvania herrerae* Baker, Hanna & Strong, 1930; *Alvania perlata* Mörch, 1860; *Alvania granti* Strong, 1938, ? = *Alvania veleronis* Hertlein & Strong, 1939; *Alvania hoodensis* Bartsch, 1911; *Alvania clarionensis* Bartsch, 1911; *Alvania ingrami* Hertlein & Strong, 1951; ? *Alvania lara* Bartsch, 1911; *Alvania nemo* Bartsch, 1915; *Alvania galapagensis* = *Alvania nigrescens* Bartsch & Rehder, 1939 [the West Indian locality for this last name is erroneous]). Caribbean (*A. chiriquiensis* Olsson & McGinty, 1958). Pleistocene, California (*Rissoina hartmanni* Jordon, 1936). Oligocene, Washington, W. coast N. America (? *Turbella cowlitzensis* Effinger, 1938).

Material examined. Types of all Recent species listed except *A. perlata*, *R. lowei* and *A. lirata*, together with numerous lots in LACM and some in USNM and AMS. Two preserved lots of *A. galapagensis* (CAS). Radulae, opercula and protoconch microsculpture examined for type species, *L. kelseyi* and *L. albolirata*.

R. hartmanni: Holotype (CAS).

T. cowlitzensis: Holotype and paratype (BPC).

Remarks. This genus has been erected to cover a group of species which are convergent with rissoid genera such as *Alvania* Risso (see Fig. 12A,E) and *Onoba* Adams (Fig. 13A) in the development of spiral and axial sculpture. Some species (such as *L. albolirata*) approach *Rissoina* Orbigny in shape (Fig. 14A), although they resemble more closely species of *Fictonoba*, a genus of Barleeinae which includes 3 species from northern New Zealand and the Kermadec Islands. The species of *Fictonoba* differ from those of *Lirobarleeia* (and *Barleeia*) in having a radula with more triangular central teeth and more finely cusped lateral teeth. In addition, the protoconch sculpture is of a different type of pitting, being much denser and more irregular. There are also anatomical differences between the type species in both genera.

Lirobarleeia differs from *Protobarleeia* in that the species it contains are much larger, and have more elongate shells, different protoconch microsculpture and a red, not yellow, operculum.

Assuming that the anatomy of *L. galapagensis* is typical of the group, *Lirobarleeia* differs from *Barleeia* in having only one female genital opening and in the ventral wall of the capsule gland being thin-walled, not thickly glandular as it is in *Barleeia*. The two genera, in other non-shell characters, are very similar. Their shells, however, differ markedly: the shells of most species of *Lirobarleeia* are strongly sculptured (not smooth) and more elongate-conic, and have thickened apertures with an orthocline to weakly opisthocline (instead of prosocline) outer lip.

Genus *Caelatura* Conrad, 1865

Caelatura Conrad, 1865a: 28 (not Fischer, 1883). Type species *Pasithea sulcata* Lea, 1833; here designated. Eocene, Alabama, U.S.A. (Fig. 15F-I).
not *Coelatura* Conrad, 1853 nor Pfeiffer, 1877.

Diagnosis. *Shell:* Small (2–3.5 mm in length), solid, elongate-conic, non-umbilicate, with spiral or axial ribs or smooth. Aperture with simple peristome, oval, subangled but not notched posteriorly, usually with varix behind sharp opisthocline outer lip. Teleoconch with strong, rounded spiral ridges, or with axial ribs, or smooth; microsculpture of irregular, minute pits (Figs 15A,B,F,H,I; 16A,B). Protoconch paucispiral, smooth (?) or with weak spiral lines; microsculpture (known only in Recent species) of very closely-packed, minute, irregular pits (Figs 15C-E,G; 16C).

Head-foot and anatomy: Unknown.

Operculum: As in *Barleeia* (Fig. 16D).

Radula: Central teeth $\frac{3+1+3}{1}$, cusps sharp, median cusp narrowly triangular; basal denticles overlap upper edge of tooth in front; lateral margins thickened, at about 45°. Lateral teeth 3 + 1 + 6–7; cusps small, primary cusp narrowly triangular, sharp. Marginal teeth with numerous, small cusps on outer edge of inner marginal teeth and outer marginal teeth (inner edge of outer marginal teeth obscured in mounts) (Fig. 16E,F).

Distribution. Eocene, south-eastern U.S.A. (*P. sulcata*). Western Atlantic (*Rissoa (Cingula) rustica* Watson, 1886 = *Alaba conoidea* Dall, 1889; *Rissoa (Cingula) pernambucensis* Watson, 1886; *Rissoa microstoma* Watson, 1886).

Material examined.

†*P. sulcata*: Types and one other lot (ANSP).

R. (C.) rustica: Syntypes (BMNH).

†*A. conoidea*: Syntypes (many) (USNM).

R. (C.) pernambucensis: Syntypes (BMNH).

†*R. microstoma*: Syntypes (BMNH), one lot (USNM).

Remarks: Palmer (1937) discussed the complex nomenclatural problems of the interpretation of the type species and its designation in relation to this genus name and *Actaeonema* Conrad, 1865 (see below). She argued that *Actaeonema* was a replacement name for “*Caelatura* Conrad 1865, nec *Caelatura* Martens”—with the type, by subsequent designation by Cossmann

(1893), "*Actaeonema striata* Conrad" which Cossmann considered, incorrectly, to be the same as *Pasithea sulcata* Lea. Palmer's interpretation is not entirely satisfactory because Conrad (1865b) erected *Actaeonema* for *Caelatura* Conrad (1865a) introduced on p. 35 under the Acteonidae. Conrad, in the same article (1865a), had also introduced *Caelatura* under the "Terebridae" on p. 28. The latter introduction has page priority and includes 2 species, *Pasithea sulcata* Lea and *Pasithea striata* Lea. The *Actaeonema* introduced on p. 35 includes only *Pasithea striata*. It is most probable that Conrad, realising his error in introducing the same name twice, proposed a substitute name for the second introduction (p. 35). The inclusion of *P. striata* under both generic names is possibly a *lapsus*, the first name (*Caelatura*, p. 28) possibly being intended for *P. sulcata* alone.

Palmer (1937) has shown that *Pasithea striata* Lea (not Conrad, 1865b) is possibly a turritellid protoconch (Palmer, p. 68, pl. 82, fig. 6). It is my contention that *Actaeonema* must have *Pasithea striata* as its type species by monotypy, as this is the only species name mentioned on page 35 under *Caelatura*. Conrad's (1865b, pl. 11, fig. 2) figure of *A. striata* is clearly not *Pasithea striata* Lea, nor is it like *Pasithea sulcata*, having fewer and weaker spiral ridges; more convex whorls, a rounded, not subangled, periphery and a larger and differently-shaped aperture. Palmer (1937, p. 156) suggests that *A. striata* of Conrad is *Tuba cancellata*, a mathildiid. The earlier introduction of *Caelatura* (p. 28) also included *Pasithea striata* but *Pasithea sulcata* is here designated as the type species.

The relationships of the type-species of *Caelatura* are somewhat obscure. It is similar to the rissoid genus *Lironoba* Iredale, 1915 in most shell features although differing in having a simple peristome. The apparently-smooth, paucispiral protoconch was slightly worn in the best specimen available and it was not definitely established whether a microsculpture was present. The teleoconch is unusual in having a microsculpture of minute punctures. The overall shell features suggest a possible relationship with *Lirobarleeia* but these two groups differ in that *Caelatura sulcata* has minute punctures over the teleoconch surface, a more expanded inner lip and stronger spiral lirae. *Protobarleeia* also differs from *Caelatura sulcata* in the characters outlined above and in possessing a spirally-sculptured protoconch.

The Recent species listed above as belonging to this genus are placed here because they possess a similar teleoconch microsculpture (observed in syntypes of *A. conoidea* [= *rustica*] and *R. microstoma*; compare Figures 15H,I with 15B and 16B) and are also similar in their apertural characters and shell outlines. The Recent species are smooth to axially ribbed, a major departure from the strong spiral keels of *C. sulcata*. Given the variation in sculpture in barleeid genera such as *Lirobarleeia* and *Pisinna* and the lack of other characters that could be used to separate them, it seems reasonable to regard those species as congeneric.

The species included herein in *Caelatura* differ from other Barleeinae in their pitted teleoconch surface, shallow irregular protoconch microsculpture and, in the one species where it is known, in radular characters. The radula of *C. rustica* has more numerous, sharper cusps than other Barleeinae and the central teeth lack a U-shaped basal projection on the face of each tooth. This structure appears to have been replaced functionally by the basal cusps overlapping the edge of the tooth in front.

Genus *Fictonoba* Ponder, 1967

Fictonoba Ponder, 1967: 212. Type species *Rissoa carnososa* Webster, 1905; by original designation. Recent, northern New Zealand (Fig. 17).

Diagnosis. *Shell:* Small (2.5–3.5 mm in length), elongate-ovate, solid, non-umbilicate, with axial and sometimes spiral sculpture; axial ribs do not extend over base. Aperture oval, rounded anteriorly, with sharp posterior angulation but lacking distinct channel, peristome simple; outer lip slightly opisthocline to orthocline, rather thin, varix absent (Fig. 17A). Protoconch dome-shaped, paucispiral, with indistinct spiral elements; microsculpture of dense, irregular pits (Fig. 17D,E). Inner chitinous layer rather poorly developed.

Head-foot: Cephalic tentacles long, slender, not tapering, eyes in swellings at their outer bases. Snout long, bilobed, very extensile. Foot long, with anterior pedal gland; no posterior pedal gland. Metapodial tentacle short, triangular. A small posterior pallial tentacle present (Ponder, 1967: pl. 5, figs 2, 3, 7).

Anatomy: Oesophageal pouches absent. Female genitalia with thin-walled ventral channel, no separate spermathecal opening, seminal receptacle on right side of albumen gland and a large bursa copulatrix present. Male with complexly lobed penis (Fig. 4F,G), open prostate gland (Fig. 4H), pallial vas deferens and penial duct (*F. carnososa*) (see anatomical account for further details).

Operculum: Very similar to that of *Barleeia*, red or yellow and red (previously described and figured by Ponder, 1967) (Fig. 17B,C).

Radula: Central teeth $\frac{2}{1} + \frac{1}{1} + \frac{2}{1}$, lateral margins considerably thickened, at about 45°; cutting edge slightly less than half width of tooth, median cusp narrow, sharp, about twice as long as adjacent cusps; basal denticles prominent; middle part of face thickened to form U-shaped projection. Lateral teeth 2–3 + 1 + 4–6; cusps sharp, primary cusp triangular, much larger than other cusps. Marginal teeth with several small cusps, subequal on both inner and outer marginals, distal cusps larger than others; cusps on outer edge of inner marginal teeth and inner and outer edges of outer marginal teeth (Fig. 17F,G).

Distribution. New Zealand (*F. carnososa*; *Rissoina rufolactea* Suter, 1908). Kermadec Islands (*Austronoba oliveri* Powell, 1926). Burdwood Bank, near Falkland

Islands, Subantarctic (? *Onoba cymatodes* Melvill & Standen, 1916).

Material examined.

†**R. carnosus*: Several lots (AMS).

†**R. rufolactea*: Paratypes and several other lots (AMS).

R. oliveri: Several lots (AMS).

O. cymatodes: Holotype (RSM).

Remarks: This genus resembles *Barleeia* in its operculum, in having a punctate protoconch microsculpture and chitinous inner shell layer. It differs from *Barleeia* and other Barleidae in having a metapodial and a posterior pallial tentacle. It also differs from *Barleeia* in the details of the central teeth of the radula, in the pattern of protoconch microsculpture, in lacking a posterior pedal gland and in several anatomical characters. The shell shape and sculpture are similar to that of species of *Lirobarleeia* but the two groups can readily be distinguished on radular characters, *Fictonoba* having smaller cusps on all teeth and a differently constructed central tooth (compare Fig. 17G with Figs 12B, 13G and 14F).

The presence of a metapodial and a pallial tentacle and the lack of a posterior mucous gland are characters that are shared with several genera of Rissoidae (Ponder, 1967). In addition the anatomy of the male and female genital systems is superficially similar to that of *Rissoina* Orbigny. *Fictonoba carnosus* has a partially separated albumen gland but lacks the true upper oviduct gland that is characteristic of the Rissoidae. Its radula, too, is superficially similar to the normal rissoid pattern (although that of *Caelatura* is more similar) and differs at sight from that of *Barleeia*. It has no jaws and in this respect resembles some other Barleidae, all Rissoidae apparently possessing well-developed jaws. The oesophagus is like that of species of Rissoidae in having short dorsal folds and in lacking oesophageal pouches. *Fictonoba*, like some species of *Rissoina*, appears to feed selectively on Foraminifera (Ponder, 1967), in contrast to the microherbivorous feeding of *Barleeia*. The stomachs of sectioned specimens of *Fictonoba* contained forams, some diatoms and fine detritus.

Fictonoba thus has characters shared by both the Barleidae and Rissoidae. An analysis of the characters and states, listed in Table 1, that are possessed by *Fictonoba*, shows that it has more characters in common with the Barleidae than with the Rissoidae (12 character states shared with Rissoidae, 14 with Barleidae). *Fictonoba* is possibly close to the stem from which the Barleidae and ancient rissoid genera such as *Rissoina* diverged, although it is also possible that the similarity between *Fictonoba* and *Rissoina* is due to convergence.

Subfamily ANABATHRINAE Coan, 1964

(*nom. correctum* Keen, 1971, for Anabathroninae)

Synonym: AMPHITHALAMIDAE (Ponder MS) Voorwinde, 1966: 41.

Diagnosis. Shell: Small or minute, elongately pupoid to broadly ovate, solid, with inner chitinous layer usually well developed, opaque, umbilicate to non-umbilicate. Aperture with simple or duplicated peristome, usually not channelled; outer lip with or without varix, prosocline to opisthocline. Teleoconch smooth or with spiral or axial sculpture, rarely both. Protoconch dome-shaped, paucispiral, usually sculptured with minute pits typically arranged in spiral rows.

Head-foot: Snout short, bilobed; foot short, with anterior pedal gland and with or without posterior pedal gland. Cephalic tentacles short, typically ciliated, usually paddle-shaped.

Anatomy: Male with penis usually attached to midline and coiled when at rest. Prostate gland closed, in and/or behind pallial cavity. Bursa copulatrix and seminal receptacle present; bursa on left (inner) side of albumen gland, seminal receptacle posterior and alongside albumen gland. Oviduct with a single distal opening or with an additional, posterior spermathecal opening. Oesophageal pouches and oesophageal gland absent (although rudimentary gland appears to be present in some species); mid-oesophagus with long dorsal folds.

Operculum: Oval, composed of two layers, nucleus eccentric, smooth or with raised ridge near inner (columellar) edge on inner side, or with short peg arising from nucleus (also an accessory peg in one genus); peg rudimentary in some species.

Radula: Variable, ranging from all teeth multicuspate with small cusps and similar to Rissoidae, to rather short teeth with few, large cusps. Central teeth with a pair of basal processes, triangular cutting edge, lateral margins at 45° or less; face with convex ventral margin but no separate U-shaped projection. Lateral teeth with few to several cusps on distal ends and distal 1/4–1/3 of outer edge of inner marginal teeth and inner edge of outer marginal teeth.

Remarks. The Anabathrinae can be readily distinguished from the Barleidae by their flat, 2-layered operculum which usually does not bear a peg. The shells are typically very small and solid. The penis is coiled whereas it is straight in the Barleidae. *Pisinna* species and *Amphithalamus incidatus* (Frauenfeld) have a spermathecal opening in the posterior part of the pallial cavity so that no important differences appear to occur in the female genitalia. It is very probable, however, that the diallic condition in *Barleeia*, and *Pisinna* and *Amphithalamus*, has been derived independently. (See 'Discussion'.) The cephalic tentacles are usually prominently ciliated and paddle-shaped, being in marked contrast to the narrow, tapering, indistinctly ciliated tentacles of *Barleeia*. The radula in the Anabathrinae lacks the U-shaped projection seen on the face of the central teeth of all genera of Barleidae except *Caelatura*, and the outer marginal teeth have cusps on their outer edges in the Barleidae but not in the Anabathrinae.

Ponder (1968) incorrectly identified an oesophageal gland in this group. The species investigated, however, have rather long dorsal folds in the midoesophagus and there is little trace of an oesophageal gland. The large number of characters listed in the family diagnosis common to the Barleeinae and Anabathrinae suggest that they are closely related and require no more than subfamily distinction (see Table 1 for list of some important characters and character states separating the two subfamilies).

This group is centred in the Southern Hemisphere, particularly in Australasia, whereas the Barleeinae have their centre of diversity in western North and Central America.

General Anatomical Account of the Anabathrinae

The following anatomical information has been obtained from the examination of the species listed: *Anabathron* (*Anabathron*) *contabulatum* (Frauenfeld), Sydney, NSW, *A. (Scrobs)* *hedleyi* (Sute) (from Ponder 1968), *Amphithalamus incidatus* (Frauenfeld), Sydney, NSW, *Pisinna semiplicata* (Powell) (from Ponder, 1968), *P. olivacea* (Frauenfeld) and *P. albizona* (Laseron), Sydney, NSW, *P. zosterophila* (Webster) (from Ponder, 1968), and *Badepigrus pupoides* (Adams), Port Hacking, NSW.

The pallial cavity. All of the species examined have a ctenidium with finger-shaped filaments. The osphradium is elongately oval, and is surrounded by a ciliated ridge. A hypobranchial gland is present and is well developed on the posterior mantle roof.

The pedal glands. The anterior pedal gland is a compact mass which extends to just below the buccal mass. The posterior pedal gland, when present, opens by way of a longitudinal slit to the sole of the metapodium and occupies much of the tissue of the foot.

The alimentary canal. The buccal cavity contains a well-developed odontophore, with a pair of odontophoral cartilages. A pair of very weak jaws is present in *Pisinna albizona* and *P. olivacea* but they have not been confirmed in *P. semiplicata* and *P. zosterophila*. *Anabathron contabulatum* and *Amphithalamus incidatus* also have weak jaws which, like those in the two species of *Pisinna*, are composed of a few chitinous rodlets. *Badepigrus pupoides* and *A. (Scrobs)* *hedleyi* apparently lack jaws.

The anterior oesophagus is rather wide and contains a pair of long, straight dorsal folds. There are no oesophageal pouches. The oesophagus passes virtually unchanged through the nerve ring and the conspicuous dorsal folds continue throughout the mid-oesophagus for approximately half the length of the cephalic cavity. There is no oesophageal gland but the tissue on the lateral walls of the anterior oesophagus of *Pisinna albizona* (the largest species sectioned) has irregular apices and resembles the tissue found in the oesophageal pouches of the Barleeinae. In other species the epithelium is more regular and consists mostly of

cuboidal cells. The posterior oesophagus is a simple, narrow tube.

The spacious stomach (Fig. 3C,D) has a rather long style sac (Fig. 3: ss) (about equal in length to the remainder of the stomach), which contains a crystalline style, and has a single digestive gland opening (*do*). The excretory cells of the digestive gland did not contain brown secretory granules except in *Pisinna olivacea*.

The intestine curves around the style sac and back towards the anterior edge of the anterior gastric chamber and then runs anteriorly. The rectum passes more or less straight along the right mantle wall to open a little behind the mantle edge.

The renal organ. The renal organ differs from that of the Barleeinae in lacking any prominent thickening (nephridial gland) on the outside wall, the epithelium being simple and composed of a single layer of cells throughout. The renal opening is simple and at the posterior end of the pallial cavity.

The nervous system. The nervous systems of the species investigated were not studied except to note the marked concentration of the circumoesophageal ganglia.

The male genital system (Fig. 8). The testis is not distinctly lobulate and lies above the digestive gland, but does not occupy the last $\frac{1}{3}$ –1 whorl of the visceral coil.

The coiled, expanded seminal vesicle appears to contain only typical (eupyrene) sperm and lies behind and/or across the inner (ventral), posterior end of the stomach. The bean-shaped prostate gland is partly embedded in the kidney wall and partly in the pallial wall in all the species examined. The lumen is a central slit, glandular above and below in species of *Pisinna*, but displaced ventrally in *Anabathron contabulatum*. There is a short ventral slit open to the pallial cavity immediately in front of the posterior pallial wall in *A. contabulatum*. A small posterior pallial opening in *Amphithalamus incidatus* was observed but none was present in *Pisinna albizona* or in the two species of *Pisinna* examined by Ponder (1968). The prostate of *P. olivacea* was badly shattered in the 3 sectioned males and, although a pallial opening was not observed, its absence could not be verified. The pallial vas deferens emerges from the distal end of the prostate gland, or just behind the distal end (as in *A. incidatus*) and the visceral vas deferens enters just behind the posterior pallial wall in all of the species examined. The pallial vas deferens is a narrow, ciliated tube which runs immediately beneath the epithelium on the neck where a few coils or undulations occur before it enters the base of the penis.

The penis is situated at about the midline of the head just behind the eyes and when at rest is coiled (Fig. 8A-C) or U-shaped (Fig. 8D). It is approximately the same length as the pallial cavity when straightened. The penial duct is simple, ciliated, and has a thin, muscular coat. The penial epithelium does not contain conspicuous gland cells except in *P. semiplicata*, which has a zone

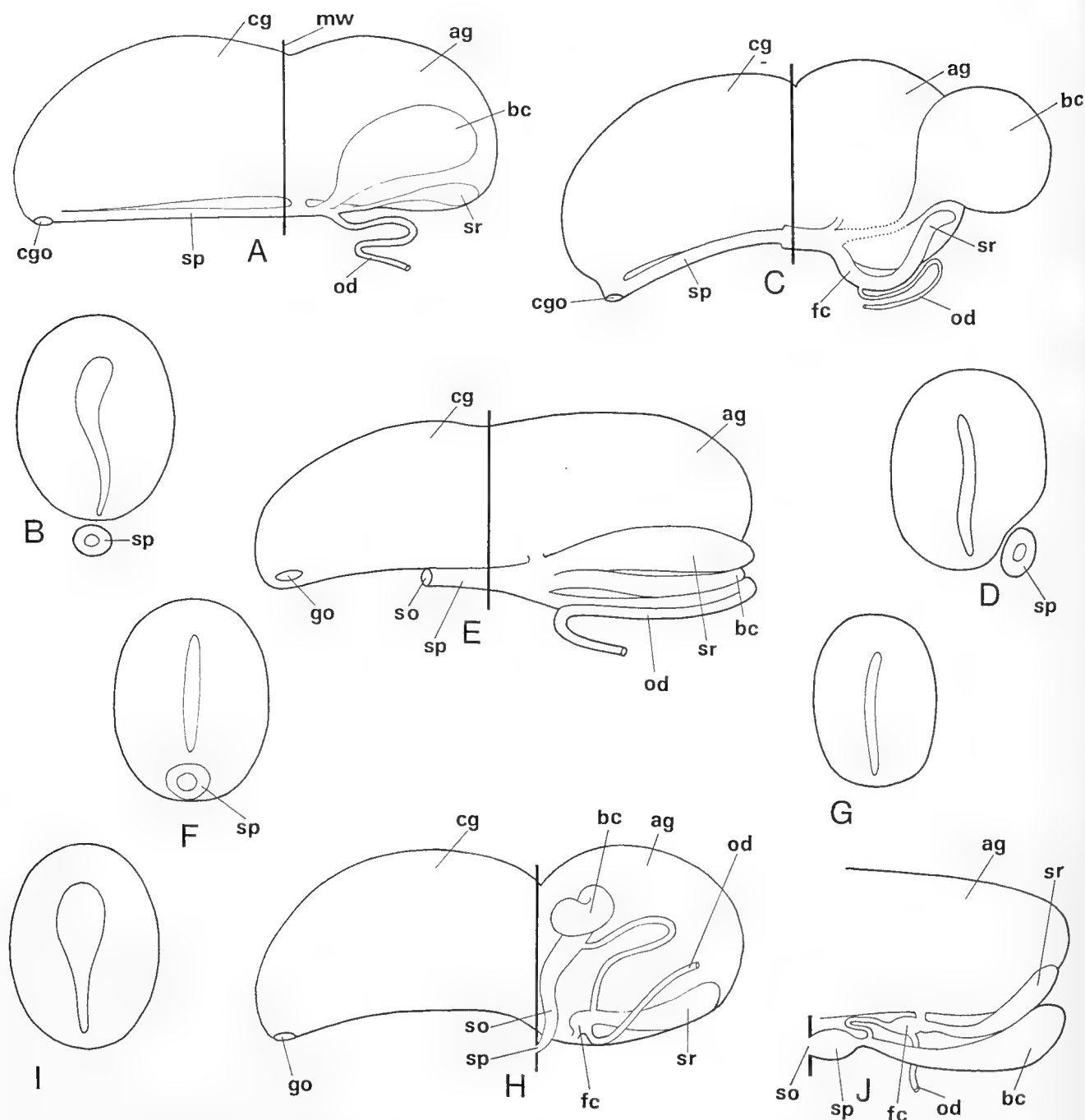


Fig. 7. Semidiagrammatic representations of the female genital systems of some Anabathrinae as seen from the left (inner) side with sections through the middle part of the capsule gland. A & B, *Badepigrus pupoides* (Adams). C & D, *Anabathron (Anabathron) contabulatum* (Frauenfeld). E-G, *Amphithalamus (Amphithalamus) incidatus* (Frauenfeld). F, section through the posterior end of the capsule gland; G, section through the anterior part of the capsule gland. H & I, *Pisinna semiplicata* (Powell). J, *Pisinna olivacea* (Frauenfeld), showing the posterior part of the oviduct glands and the sperm sacs.

ag, albumen gland; bc, bursa copulatrix; cg, capsule gland; cgo, common genital opening; fc, fertilization chamber; go, oviductal opening; mw, posterior pallial wall; od, upper oviduct; so, spermathecal opening; sp, spermathecal tube; sr, seminal receptacle.

of long, glandular epithelial cells. These were incorrectly interpreted as prostatic cells by Ponder (1968, fig. 16). The penial opening is situated at the pointed, distal end of the penis.

The female genital system (Fig. 7). The ovary is simple, is short compared with the digestive gland, and

contains large, yolky eggs. The narrow, thin-walled upper oviduct becomes ciliated as it approaches the oviduct glands but does not noticeably thicken externally. In *A. incidatus*, *B. pupoides* and *A. contabulatum* the oviduct (Fig. 7: od) forms a tight loop ventral to the sperm sacs. The histology of the distal

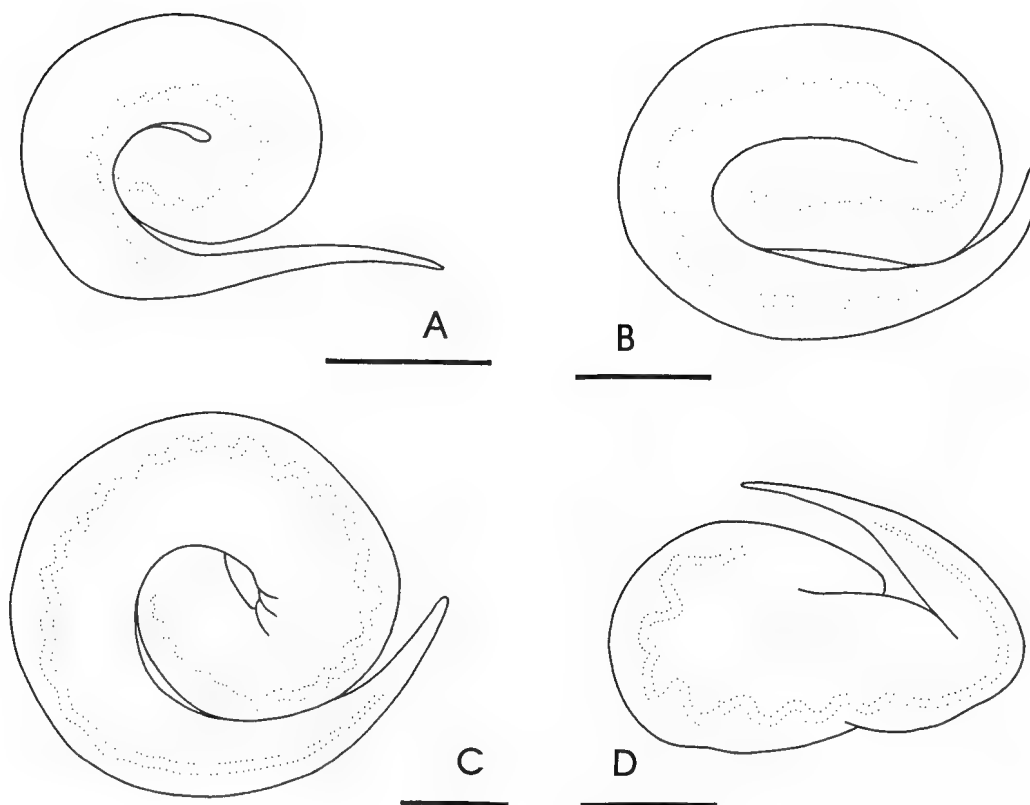


Fig. 8. Penes of the Anabathrinae. **A**, *Anabathron (Anabathron) contabulatum* (Frauenfeld); Fingal Head, Port Stephens, NSW. **B**, *Amphithalamus (Amphithalamus) incidatus* (Frauenfeld); Fingal Head, Port Stephens, NSW. **C**, *Pisinna olivacea* (Frauenfeld); Fairlight, Sydney, NSW. **D**, *Badepigrus pupoides* (Adams); Port Hacking, NSW. Scale: 0.1 mm.

arm is different from that of the proximal arm in *A. incidatus*, consisting of an irregular epithelium containing a few blue-staining cuboidal cells and ciliated cells. The proximal arm is lined with a regular cuboidal, ciliated epithelium.

The oviduct opens to a small, ciliated fertilization area (Fig. 7: *fc*) into which the seminal receptacle and the bursa copulatrix, which lie on the left side of the albumen gland, also open. In *Amphithalamus incidatus* (Fig. 7E) this area is muscular and the short ducts of the sperm sacs are contained in a common muscular sheath. In this species the thin-walled seminal receptacle (Fig. 7E: *sr*) is larger than, and lies dorsal to, the muscular bursa copulatrix (Fig. 7: *bc*) and the two sacs are bound together with connective tissue. The seminal receptacle contains orientated sperm lying in its lumen, whereas the bursa copulatrix was not observed to contain sperm in any of the specimens sectioned. The seminal receptacle is lined with pavement epithelium and surrounded by a thin layer of muscle fibres. The bursa has a thickly muscular wall and is lined with ciliated, cuboidal cells thrown into low longitudinal ridges.

In *Anabathron contabulatum* (Fig. 7C) the bursa copulatrix (Fig. 7C: *bc*) is larger than the seminal receptacle (Fig. 7C: *sr*) which lies ventral to it. The seminal receptacle is a long narrow sac with thin walls

and opens to the oviduct proximal to the bursal opening. The tubular fertilization area (Fig. 7C: *fc*) is lined with short, orange-staining gland (?) cells. At the point where it receives the bursal duct the oviduct opens to the albumen gland. It then becomes tubular and is lined with relatively large, cuboidal, pale-blue-staining cells and has a very narrow lumen. The large, ovoid bursa copulatrix (Fig. 7C: *bc*) is lined with columnar cells and contains unorientated sperm. Its duct is surrounded by the albumen gland. The arrangement of the sperm sacs and upper oviduct in *Anabathron (Scrobs) hedleyi* is similar to that of *A. contabulatum* but differs in having the bursal duct free of the albumen gland.

Badepigrus pupoides (Fig. 7A) has fertilization area and sperm sacs similar to *A. contabulatum* and *A. (S.) hedleyi*, the main difference being that the seminal receptacle (Fig. 7A: *sr*) opens immediately behind the bursal duct (which is not embedded in the albumen gland).

In species of *Pisinna* the fertilization area (Fig. 7H,J: *fc*) is a small sac into which opens the oviduct (Fig. 7H,J: *od*) (which does not loop as it does in the other genera) and the seminal receptacle. The bursa copulatrix (Fig. 7H,J: *bc*) is connected to this area by a rather long, narrow duct. The seminal receptacle (Fig. 7H,J: *sr*) is a long, tubular, thin-walled structure similar to that seen

in *A. contabulatum*, *A. (S.) hedleyi* and *B. pupoides*, but the bursa copulatrix is rather different. It is located on the left side of the albumen gland (as it is in the other genera), lying opposite the anterior end of the gland in *P. semiplicata* and *P. albizona* but near the posterior end in *P. olivacea*. It is an elongately ovoid, muscular sac and was not observed to contain sperm. It is almost certainly homologous with the bursa copulatrix of the other genera and is similar histologically to the structure regarded as a bursa in *A. incidatus*. The distal ovoid section tapers into a long muscular tube and the narrow duct leading to the fertilization area opens a little more than half-way along its length (i.e. towards the distal end) in *P. semiplicata* and *P. albizona* (Fig. 7H) or very near the proximal end (in *P. olivacea*) (Fig. 7J). The muscular tube then opens (Fig. 7H,J: *so*) to the posterior end of the pallial cavity by way of a short spermatheca (Fig. 7H,J: *sp*) lined with ciliated and mucous cells. The spermatheca is expanded into a vestibule-like structure in *P. olivacea*.

The fertilization area in *A. incidatus* continues anteriorly as a narrow duct (Fig. 7E: *sp*) lined with large, pale-blue-staining cuboidal cells and then, after a short section lined with ciliated and mucous cells, opens to the pallial cavity a little in front of the posterior pallial wall. This opening (Fig. 7E: *go*), in species of *Pisinna*

and *A. incidatus*, can be closed with a sphincter muscle. This makes it difficult to discern in sections and I overlooked it in my (1968) account of *P. semiplicata*.

In *Badepigrus pupoides* and *Anabathron contabulatum* a short section of the narrow sperm tube is also lined with pale-blue-staining cells (similar to those seen in the other genera) in the region immediately anterior to the fertilization area. This tube continues anteriorly as a ciliated spermathecal duct (Fig. 7A–D: *sp*) lying beneath the capsule gland and separate from it. In both species it joins with the small vestibule of the capsule gland just behind the common genital aperture (Fig. 7A,C: *cgo*).

The albumen gland (Fig. 7: *ag*) is about the size of the capsule gland (Fig. 7: *cg*) in all the species examined and the two glands are continuous. The capsule gland commences at about the posterior pallial wall, and continues along the right pallial wall to open distally at a small aperture. The capsule gland is oval in section and thin ventrally in *Anabathron contabulatum* (Fig. 7D) and *Badepigrus pupoides* (Fig. 7B). It has a slightly thicker ventral wall in *Pisinna* species (Fig. 7I) and, in *Amphithalamus incidatus*, a thick ventral wall posteriorly (Fig. 7F) which becomes thinner anteriorly (Fig. 7G).

Key to the Genera and Subgenera of the Anabathrinae

1. Shell with cleft between aperture and inner lip closed by callus behind posterior corner of aperture 2
 - Shell with inner lip of aperture fused to parietal wall or separated from it; lacking a callus behind posterior corner of aperture 4
2. Shell minute (less than 1.6 mm in length), usually red, purple, pinkish, pale yellow or white; foot lacking posterior mucous gland *Anabathron* (*Scrobs*)
 - Shell minute to small (greater than 1 mm in length), usually brown, yellow or reddish-brown; foot with posterior mucous gland (*Amphithalamus*) 3
3. Shell with prominent axial and/or spiral sculpture *Amphithalamus* (*Notoscrobs*)
 - Shell smooth or with a peripheral groove or cord *Amphithalamus* s.s.
4. Shell minute (less than 1.6 mm in length), elongate-pupoid, whorls smooth except for median keel *Anabathron* s.s.
 - Shell small to minute (more or less than 1.6 mm in length), smooth or with various sculpture (but not elongate-pupoid and smooth with median keel) 5
5. Shell variously sculptured, with circular to subcircular aperture with broad inner lip firmly attached to, and spread over, parietal wall *Pisinna*
 - Shell variously sculptured, with narrow inner lip attached to or separated from parietal wall 6
6. Shell pupiform, smooth or spirally sculptured, aperture D-shaped, inner lip attached to parietal wall *Microdryas*
 - Shell variously shaped, smooth or variously sculptured; aperture oval to subcircular, inner lip attached to parietal wall or separated from it 7
7. Operculum with 1 or 2 pegs, shell shape and sculpture various 8
 - Operculum simple, shell ovate-conic to conic, smooth *Pseudestea*

8. Operculum with 1 very short peg, peristome usually duplicated, shell pupiform to trochiform, smooth or with axial sculpture or spiral keels *Afriscrobs* n.gen.
- Operculum with 2 pegs, peristome duplicated, shell pupiform, with evenly convex whorls and fine spiral threads *Nodulus*

Genus *Anabathron* Frauenfeld, 1867

Anabathron Frauenfeld, 1867: 13. Type species *Anabathron contabulata* Frauenfeld, 1867 (= *contabulatum* emend.); by monotypy. Recent, south-eastern Australia (Figs 1E; 7C,D; 8A; 18E-H).

Diagnosis. Shell: Shell minute (1–1.5 mm), solid, ovate to elongate-pupoid, non-umbilicate, usually red, pink or yellowish, with or without distinct cleft between inner lip and parietal wall, smooth, with spiral cords, threads or grooves, or with strong spiral keel. Aperture oval, not angled or channelled, with duplicated peristome, outer lip orthocline to slightly prosocline. Protoconch paucispiral, dome-shaped, with spiral rows of minute pits. Inner chitinous layer well developed.

Head-foot: Unpigmented; with paddle-shaped cephalic tentacles bearing long, immobile setae; foot with anterior and posterior pedal glands, or posterior pedal gland absent. Penis simple, coiled, attached to midline of head.

Anatomy: Female genital duct monaulic (Fig. 7C,D); penis simple, coiled, attached to middle of head (Fig. 8A).

Operculum: Oval, of two layers, inner surface with a raised ridge just inside inner (columellar) edge; sometimes a small swelling just inside ridge.

Radula: Central teeth $\frac{(3-2) + 1 + 2(-3)}{1}$, with long, narrow, sharp cusps; cutting edge slightly more than width of tooth; basal denticles near outer edge of each tooth, well developed; lateral margins narrow, at about 45°, well separated from rest of base; ventral margin of tooth with tongue-like extension. Lateral teeth 2–3 + 1 + 3, with long, sharp cusps. Marginal teeth simple, curved, with rather long, sharp cusps, inner marginal teeth with almost straight cutting edge at right angles to rest of tooth.

Remarks. Ponder (1967) tentatively retained *Anabathron* and *Scrobs* as distinct genera while noting their close relationship. Examination of living material shows that species of *Anabathron* have a very similar external appearance to those of *Scrobs*, differing only in species of *Anabathron* s.s. having a posterior pedal gland. In view of this and the extremely close similarity of the anatomy, radula and operculum, *Scrobs* is here considered to be only subgenerically separable from *Anabathron*.

Subgenus *Anabathron* s.s.

Diagnosis. Shell: As for genus but with a single spiral keel on each whorl causing a strong angulation,

and a weaker cord on base. Inner lip of aperture only slightly separated from parietal wall (Fig. 18E-H).

Head-foot: As for genus; with posterior pedal gland opening to a longitudinal groove in sole (*A. contabulatum* and *A. lene*, Sydney, New South Wales, Australia) (Fig. 1E).

Operculum: As for genus, inner surface with a small raised area just inside ridge near columellar edge (Fig. 18G).

Radula: As for genus (Fig. 18H).

Distribution. Australia (*A. contabulatum*; *Anabathron contabulatum lene* Hedley, 1918).

Material examined.

†**A. (A.) contabulatum*: Types (NHMV) and many other lots (AMS).

†**A. contabulatum lene*: Types (NHMV) and many other lots (AMS).

Remarks. This subgenus contains only the type species and a very similar sympatric species, *A. lene*. They never intergrade, are easily distinguished from each other and are not sexually dimorphic forms of one species. The typical subgenus is distinguished from the next by the strongly keeled shell which has a very narrow groove between the inner lip and the parietal wall, and in having a posterior pedal gland in the foot.

Subgenus *Scrobs* Watson, 1886

Scrobs Watson, 1886: 611. Type species *Rissoa (Scrobs) scrobiculata* Watson, 1886; by subsequent designation by Cossmann, 1921:36. Recent, south-eastern Australia (Fig. 19A,B).

Nannoscrobs Finlay, 1927: 377. Type species *Amphithalamus hedleyi* Suter, 1908; by original designation. Recent, New Zealand (Fig. 19C-F).

Ultisrobs Iredale, 1955: 81. Type species *Scrobs pluteus* Laceron, 1950; by original designation. Recent, south-eastern Australia (Fig. 19G).

Diagnosis. Shell: As for genus but with distinct channel between inner lip and parietal wall. Whorls rarely angled, sculpture, if present, usually weak, sometimes of spiral lirae or threads (Figs 18A; 19A-D,G).

Head-foot: As for genus; posterior pedal gland absent (Ponder, 1967; *A. (S.) luteofuscus*, Sydney; New South Wales, Australia. *A. (S.) hedleyi*, Ponder, 1967, 1968) (Fig. 1F).

Operculum: As for genus but lacking small raised area inside ridge at columellar edge (Ponder, 1967) (Figs 18B, 19E).

Radula: As for genus (Figs 18C,D; 19F).

Distribution. South-eastern and southern Australia (*R. [S.] scrobiculator*; *S. pluteus*; *Amphithalamus luteofuscus* May, 1919 = *Scrobs delta* Laseron, 1950); New Zealand (*A. hedleyi* and several other species [see Powell, 1979]).

Material examined.

†*R. (S.) scrobiculator*: Holotype (BMNH) and a few other lots (AMS).

†*A. hedleyi*: Several lots (AMS, NMNZ).

†*S. pluteus*: Syntypes and a few other lots (AMS).

†*A. luteofuscus*: Holotype (TM) and many other lots (AMS).

S. delta: Syntypes (AMS).

Several other New Zealand and temperate Australian species have also been examined.

Remarks. Ponder (1967) placed *Nannoscrobs* in the synonymy of *Scrobs* and *Ultisrobs* in the synonymy of *Microfossa* (= *Amphithalamus*). Examination of the shell of the type species of *Ultisrobs* indicates that it is a *Scrobs*, not an *Amphithalamus*. There is, however, a sympatric, undescribed species of *Amphithalamus* which is superficially very similar to *S. pluteus*. Ponder (1968) described the anatomy of *A. (S.) hedleyi* which is similar to that of *Anabathron contabulatum*. Although the presence of a spermathecal tube ventral to the capsule gland was not recorded, the absence of this structure needs to be confirmed.

Genus *Amphithalamus* Carpenter, 1864

Amphithalamus Carpenter, 1864: 656. Type species

Amphithalamus inclusus Carpenter, 1864; by monotypy.

Recent, California (Fig. 20A–D).

Amphithalmus err. auct.

Diagnosis. *Shell*: Small (1–2 mm in length), solid, ovate-conic to elongate-conic, non-umbilicate with well-developed pit between inner lip and parietal wall. A callus plug at suture terminates posterior end of pit. Teleoconch usually smooth, sometimes with axial and spiral cords (subgenus *Notoscrobs*), or with weak peripheral cord or groove. Aperture oval, not channelled or angled, peristome simple or weakly-duplicated; outer lip orthocline to slightly prosocline. Protoconch paucispiral, dome-shaped; spiral rows of minute pits are the only sculpture. Inner chitinous layer well developed.

Head-foot: Pigmented or unpigmented; cephalic tentacles typical of family; anterior and posterior pedal mucous glands present, sole with posterior mucous slit. Penis simple, coiled, attached to midline behind head.

Anatomy: Female genital tract diaulic (Fig. 7E–G); penis simple, coiled, attached to midline of head behind eyes (Fig. 8B).

Operculum: Oval, thick, distinctly double-layered, often with raised lamella on inner side.

Radula: Central teeth $\frac{(3-2)2+1+2(-3)}{1}$, each with broad, blunt median cusp and small, sharp lateral cusps, a pair of small basal denticles near outer edge of each tooth and weakly thickened lateral margins at 20°–45°,

ventral margin of tooth with tongue-like extension. Lateral teeth 2 + 1 + 2–4, primary cusp blunt. Marginal teeth simple, curved, with several small cusps, inner marginal teeth with cutting edge at right angles to rest of tooth.

Remarks. This genus is superficially similar to *Anabathron* (*Scrobs*) but differs in its generally larger size, brownish rather than pinkish or purplish coloration, the presence of a mucous slit in the sole, and very different radular features. No other barleiid genus (apart from *Anabathron* (*Scrobs*)), has the aperture separated from the body whorl by a groove terminated by a callus.

Ponder (1967) tentatively retained *Amphithalamus* and *Notoscrobs* as separate genera but the investigation of the type species and other species of both genera and of *Microfossa* suggest that there is but a single generic unit recognizable.

Subgenus *Amphithalamus* s.s.

Microfossa Laseron, 1950: 267. Type species *Subanaea* [sic; = *Sabanaea*] *incidata* Frauenfeld, 1867; by original designation. Recent, south-eastern Australia (Figs 3C; 7E–G; 8B; 20E–G).

Obesrobs Iredale, 1955:81. Type species *Rissoa jacksoni* Brazier, 1895; by original designation. Recent, south-eastern Australia (Fig. 21A–D).

Diagnosis. *Shell*: As for genus but lacking prominent sculpture, having only a weak spiral thread or groove on the periphery and sometimes a spiral cord on the base (Figs 20A,B,F; 21A,C).

Head-foot: As for genus (Ponder, 1967; also observations on *A. (A.) inclusus*, Monterey, California, U.S.A., *A. (A.) vallei*, Missouri Key, Florida, *A. (A.) incidatus*, *A. (A.) pyramis* and *A. (A.) jacksoni*, Sydney, New South Wales) (Fig. 1G,H).

Operculum and radula: As for genus (Figs 20C–E,G; 21B,D).

Distribution. West America (*A. inclusus* = *Amphithalamus tenuis* Bartsch, 1911 = *Amphithalamus stephensae* Bartsch, 1927 = *Amphithalamus trosti* Strong & Hertlein, 1939). Caribbean Sea (*A. vallei* Aguayo & Jaume, 1947). South Africa (*Sabanaea neglecta* Turton, 1932). Tropical western Pacific (*Scrobs fulcra* Laseron, 1956). Temperate Australia (*S. incidata*; *R. jacksoni* = *Rissoa* (*Scrobs*) *badia* Watson, 1886 not Petterd, 1884; *Amphithalamus obesus* H. Adams, 1865 = *Estea erma* Cotton, 1944; *Scrobs pyramis* Laseron, 1950). New Zealand (4 taxa, see Powell, 1979). Miocene of Italy (*Parvisetia ?mioscrobsoides* Sacco, 1895) and Miocene of New Zealand (*Scrobs kaawaensis* Laws, 1936; *Scrobs latoscrobs* Laws, 1948).

Material examined.

†*A. inclusus*: Syntype (USNM) and several other lots (AMS).

A. tenuis: Holotype (USNM).

A. trosti: Holotype (CAS).

- †**A. vallei*: A few lots (AMS).
 †**S. fulcra*: Holotype and paratypes and many other lots (AMS).
 †**A. obesus*: Holotype (BMNH) and many other lots (AMS).
E. erma: Holotype and paratypes (SAM).
 †**S. incidata*: Types (NHMV) and many other lots (AMS).
 †**R. jacksoni*: Types (of *R. badia* Watson) (BMNH) and many other lots (AMS).
 †**S. pyramis*: Syntypes and many other lots (AMS).
S. neglecta: Type (OUM).
R. mioscroboides: Holotype (TGM).
S. kaawaensis and *S. latoscrobis*: Paratypes (AUG).

Remarks. The few named American species of *Amphithalamus* probably fall into a single species complex, being very similar and clearly very closely related. They are all very small, with or without a weak peripheral groove or cord, and usually the base is paler than the rest of the shell and bears a weak cord. The subgenus reaches its greatest diversity in temperate Australia and New Zealand where the species are generally larger than their American counterparts, are often uniformly dark brown in colour, and lack any basal cord. Intermediate forms are, however, encountered in the tropical Indo-Pacific and because of this, and because of their very similar opercular and radular features, the Australasian and American groups are here considered to be consubgeneric.

Subgenus *Notoscrobs* Powell, 1927

Notoscrobs Powell, 1927: 547. Type species *Notoscrobs ornatus* Powell, 1927; by original designation. Recent, northern New Zealand (Fig. 21E).

Diagnosis. *Shell*: As for genus but teleoconch with strong spiral cords and, often, axial ribs (Fig. 21E,G).

Head-foot: A few details given by Ponder (1967).

Anatomy: Unknown.

Operculum and radula: As for genus (Fig. 21F,H,I) (also known [Ponder, 1967] for *A. (N.) erosus*).

Distribution. Northern New Zealand (*N. ornatus*, *Rissoa erosa* Odhner, 1924) and temperate Australia (*Amphithalamus triangulus* May, 1915; *Amphithalamus liratus* Thiele, 1930). Miocene (*Notoscrobs semiornatus* Laws, 1948) and Pliocene (*Notoscrobs waitemata* Laws, 1950) of New Zealand.

Material examined.

- †*N. ornatus*: Holotype (AIM) and a few other specimens (NMNZ).
R. erosa: A few specimens (NMNZ, AMS).
A. triangulus: Holotype (TM) and a few lots (AMS).
 †**A. liratus*: Holotype (HUM) and several lots (AMS).
N. semiornatus and *N. waitemata*: Paratypes (AUG).

Remarks. This small group is retained as a separate subgenus on the basis of the heavily sculptured shells of the species it contains, which are in sharp contrast with those of the species in the typical subgenus. No species are known that show intermediate sculptural development.

Genus *Microdryas* Laseron, 1950

Microdryas Laseron, 1950: 277. Type species *Estea iravadioides* Gatliff & Gabriel, 1913, ICZN Opin. 1181. Recent, south-eastern Australia (Fig. 22A,B).

Diagnosis. *Shell*: Small (1–1.5 mm in length), elongate-pupoid, non-umbilicate, of moderate thickness, smooth, spirally striate or with weak spiral cords; aperture ovate, sub-angled posteriorly, not channelled, inner lip nearly straight, obliquely inclined, not separated from parietal wall except by an extremely narrow groove; peristome simple, outer lip orthocline to opisthocline, with or without very weak varix. (Fig. 22A–C). Protoconch dome-shaped, paucispiral, with spiral rows of minute punctures (Fig. 22D).

Head-foot: Cephalic tentacles short, broad, eyes rather small, snout short, bilobed (preserved specimen of *M. striatus* (Powell) from Ponder, 1967).

Anatomy: Not known.

Operculum: Flat, thick, transparent, columellar edge straight, nucleus small; a ridge along inner side of columellar edge (Fig. 22F). (Also known for *M. striatus* Ponder, 1967: 207, pl. 3, fig. 17.)

Radula: Central teeth $\frac{2}{1} + \frac{1}{1} + \frac{2}{1}$, cusps short, blunt; basal denticles small, laterally placed, ventral margin with tongue-like extension, lateral margins at about 30°. Lateral teeth 2 + 1 + 3, cusps short, blunt. Inner marginal teeth with long, straight cutting edge at right angles to axis of tooth bearing several (about 11) small, sharp cusps. Outer marginal teeth with hook-like distal ends (Fig. 22E).

Distribution. South-eastern Australia (*E. iravadioides*; *Microdryas* sp., Lord Howe I.). South Africa (*Nodulus innotabilis* Turton, 1932 = *Nodulus rietensis* Turton, 1932; *Nodulus rufanensis* Turton, 1932). New Zealand (*Epigrus striatus* Powell, 1927). Japan (?*Hyala pumila* A. Adams, 1870).

Material examined.

- †*E. iravadioides*: Holotype (NMV), paratypes (NMV, AMS) and several other lots (AMS).
N. innotabilis: Holotype (OUM).
N. rietensis: Holotype and paratypes (OUM).
N. rufanensis: Holotype and paratypes (OUM).
E. striatus: Holotype (AIM).
H. pumila: Possible type (NMW).
 †**M. n.sp.*: Lord Howe Island (AMS).

Remarks. Laseron (1950) designated *Cingula australiae* Frauenfeld as the type species of *Microdryas* but he misidentified Frauenfeld's species: his specimens so named are *M. iravadioides*. The shells of species in this genus differ from others in the subfamily in their

tall spire, somewhat D-shaped aperture with an almost straight inner lip, and smooth or spirally sculptured surface.

Genus *Badepigrus* Iredale, 1955

Badepigrus Iredale, 1955: 81. Type species *Rissoa badia* Petterd, 1884; by original designation. Recent, south-eastern Australia (Fig. 23A,B).

Laseronula Whitley, 1959: 60, new name for *Saltatricula* Laseron, 1956: 445, not Burmeister, 1861, new name for *Saltatrix* Laseron, 1950: 277, not Klug, 1833. Type species *Epigrus protractus* Hedley, 1904; by original designation. Recent, eastern Australia (Fig. 23C,D).

Saltratricula err. auct.

Diagnosis. *Shell:* Minute (1–1.5 mm in length), solid, elongate to pupoid, sometimes last whorl disjunct; orange-brown in colour. Teleoconch smooth except for axial growth lines, one species with 2 strong, spiral keels. Whorls usually weakly to moderately convex, sometimes sharply-angled. Aperture with simple, oval peristome, edge blunt, outer lip opisthocline, without varix; inner lip widely to slightly separated from parietal wall (Fig. 23A,C,E). Protoconch dome-shaped, of about 1½ whorls, sculptured with minute pits arranged in spiral series, each series consisting of a narrow band of irregularly arranged pits (Fig. 23B,D,F). Inner chitinous layer poorly developed.

Head-foot: Pigmented; cephalic tentacles short, parallel-sided, with rounded ends, ciliated but without immobile 'setae'. No accessory tentacles. Snout long, broad, not distinctly bilobed. Sole without posterior mucous gland; anterior pedal gland present. (*B. pupoides*, Port Hacking, New South Wales, Australia) (Fig. 11).

Anatomy: Female genital tract monaulic (Fig. 7A,B); penis simple, U-shaped when at rest, with narrow, pointed distal portion and large, broad proximal portion (Fig. 8D).

Operculum: Oval, double-layered, inner face with weak ridge on inner (columellar) edge (*B. pupoides*) (Fig. 23G).

Radula: Central teeth $\frac{(1) + 1 + (1)}{1}$ small, elongate, each with 2 prominent basal processes close together at base of tooth, cutting edge very narrow, with small, blunt median cusp and a pair of rudimentary lateral cusps; lateral margins thin, at about 15°. Lateral teeth $1 + 1 + 1$, with massive, blunt primary cusp and 2 heavy basal supports. Inner marginal teeth short, with 4–5 large cusps on distal end and a large basal process. Outer marginal teeth smaller than inner marginal teeth, lacking large cusps but cusp pattern on inner edge (if any present) obscured in mounts (Fig. 23H,I).

Distribution. South-eastern and eastern Australia (*R. badia* = *Rissoa* (*Amphithalamus*) *verconis* Tate, 1899 = *Rissoa verconis* var. *apiculata* Gatliff & Gabriel, 1913 = *Saltatricula improrsa* Laseron, 1956; *Amphithalamus pupoides* H. Adams, 1865 = *Amphithalmus* [sic] *peilyae* Nevill, 1881 = *Rissoa*

pulchella Petterd, 1884, = *Rissoa* (*Amphithalamus*) *petterdi* Brazier, 1895; *Epigrus protractus* Hedley, 1904 = *Saltatricula stringera* Laseron, 1956 = *Saltatricula ballerina* Laseron, 1956; *Anabathron contortum* Hedley, 1907; *Epigrus semicinctus* May, 1915).

Material examined.

†*R. badia*: Holotype (TM) and several other lots (AMS).

R. verconis var. *apiculata*: Syntypes (NMV).

S. improrsa: Holotype and paratypes (AMS).

†*E. protractus*: Holotype and paratype and several other lots (AMS).

S. ballerina and *S. stringera*: Types (AMS).

†**Amphithalamus pupoides*: Holotype (BMNH) and many other lots (AMS).

R. pulchella (= *R. petterdi*): Holotype (TM).

A. contortum: Syntypes and a few other lots (AMS).

E. semicinctus: Holotype (TM) and a few other lots (AMS).

Remarks. Unfortunately only the shell is known for the type species of this genus but *B. pupoides* appears to be closely related and the animal of the type species should be similar in most respects. The radula is quite distinct from that of *Amphithalamus*, *Anabathron* and *Nodulus*. The external features of the animal differ from *Amphithalamus* and *Anabathron* in the cephalic tentacles being narrower. *Badepigrus* is most closely allied to *Afriscrobs* n.gen. and is contrasted under that genus. The synonymy follows Ponder (1967).

Afriscrobs n. gen.

Type species: *Amphithalamus africanus* Bartsch, 1915. Recent, South Africa (Fig. 24A–C).

Diagnosis. *Shell:* Minute (0.8 mm–1.5 mm in length), pupoid to trochiform, non-umbilicate to umbilicate, smooth, with spiral keels, or axially ribbed. Aperture ovate to subcircular, with simple or weakly duplicated non-channelled peristome; inner lip slightly separated from, or fused to, parietal wall; outer lip orthocline to prosocline, with sharp edge, not varicose (Fig. 24A,D,G). Protoconch paucispiral, dome-shaped, sculptured with exceedingly minute puncta not arranged in spiral rows (Fig. 24E).

Head-foot and anatomy: Not known.

Operculum: Oval, with 2 layers, inner side with a short, blunt, peg-like process emerging from nucleus and a raised rim along inner (columellar) edge (Fig. 24B,F).

Radula: Central tooth $\frac{2-1+1+1-2}{1}$, with a pair of prominent basal denticles emerging from lower face; lateral margins thin at 15°–35°; cutting edge with large, triangular median cusp (blunt, broad, short in *A. saldadinensis*), and small, lateral cusps; ventral margin produced into long U-shaped extension. Lateral teeth 2–4 + 1 + 1–2, cusps sharp in most species. Inner marginal teeth with cutting edge at right angles to axis

of tooth, 1-3 + 1 + 1-3, cusp, sharp; outer marginal teeth with a few sharp cusps (Fig. 24C,H).

Distribution. South Africa (*A. africanus* = *Amphithalamus multistriatus* Turton, 1932 = *A. denseplicatus* Turton, 1932, ? = *Turritella eucosmia* Turton, 1932; *Amphithalamus muiri* Barnard, 1963; *Rissoa adjacens* Smith, 1910, ? = *Nodulus dilectus* Turton, 1932; *Solariella quantilla* Turton, 1932; ?*Alvania minutissima* Turton, 1932; *Amphithalamus turtoni* Bartsch, 1915); Red Sea (?*Nodulus saldadinensis* Hornung & Mermoud, 1928). ?Miocene, Italy (?*Nodulus tauromiocenicus* Sacco, 1895).

Material examined.

†**A. africanus*: Turton coll. (OUM) and a few other lots (AMS).

A. multistriatus: Holotype (OUM).

A. denseplicatus: Syntypes (OUM).

†**T. eucosmia*: One lot (AMS).

R. adjacens: Syntypes (BMNH).

N. dilectus: Holotype (OUM).

†**S. quantilla*: A few lots (AMS).

A. minutissima: Holotype (OUM) and a few other lots (AMS).

A. turtoni: Holotype (USNM), one other lot (OUM).

N. tauromiocenicus: Type (TGM).

†*one undescribed South African species (AMS).

Remarks. This genus is proposed for a small group of South African species having diverse shells but appearing to agree closely in radular and opercular characters. The radula shows some similarity with that of *Badepigrus*, particularly in the position of the basal denticles and in the thin lateral margins. It differs from the one species (*B. petterdi*) in that genus for which the radula is known in having a much squarer central tooth and more cusps on the lateral and inner marginal teeth. There are also more cusps on the inner side of the primary cusp of the lateral teeth than on the outer side, a feature not encountered in other genera. The operculum of *B. petterdi* lacks a peg and the aperture of all the species of *Badepigrus* has a simple, not a duplicated, peristome. *Anabathron*, *Amphithalamus*, *Nodulus*, *Microdryas* and *Pseudestea* all differ markedly in their radular and opercular characters.

Nodulus saldadinensis from the Red Sea is tentatively placed in this genus although the shell more closely resembled *Badepigrus* in its shape and simple peristome. The operculum has a very reduced peg but the radula more closely resembles that of species of *Amphithalamus*. The lateral teeth have the formula 2 + 1 + 2, this being intermediate between *Amphithalamus*, which typically has more cusps outside the primary cusp, and *Afriscrobs*, which has the reverse condition.

Genus *Pseudestea* Ponder, 1967

Pseudestea Ponder, 1967: 208. Type species *Scrobs pyramidatus* Hedley, 1903; by original designation. Recent, south-eastern Australia (Fig. 25A-E).

Diagnosis. *Shell*: Minute (1.2-1.5 mm in length), conic to ovate-conic, imperforate, smooth. Aperture oval, peristome simple, lacking channels; inner lip separated from parietal wall by simple, narrow groove; outer lip slightly opisthocline, with blunt edge, lacking varix (Fig. 25A). Protoconch large, dome-shaped, of about 1½ whorls, terminated by distinct varix; sculptured with spiral rows of minute punctures (Fig. 25B). Inner chitinous layer well developed.

Head-foot: Known only from restored dried animal. Pigmented; cephalic tentacles short, blunt, eyes at their outer bases, of medium size. Snout short, broad, bilobed. Sole with posterior mucous groove. (From Ponder, 1967.)

Anatomy: Penis of about 1 coil, attached to midline of head, distal ⅓ swollen and with about 11 chitinous spines, the proximal ones largest (from Ponder, 1967).

Operculum: Oval, simple, of two layers, with low ridge just inside columellar edge and small, low knob-like thickening at nucleus on inner surface (Fig. 25C).

Radula: Central tooth $\frac{3+1+3}{1+1+1}$, median cusp narrow, sharp, lateral cusps small, sharp; basal denticles prominent, extend beyond ventral margin; ventral margin U-shaped, lateral margins weakly thickened, at about 15°. Lateral teeth 4 + 1 + 6-7, primary cusp large, sharp, lateral cusps small, sharp. Marginal teeth with numerous small sharp cusps, cutting edges curved (Fig. 25D,E).

Distribution. Southern and south-eastern Australia (*S. pyramidatus*) and northern New Zealand (*Scrobs crassiconus* Powell, 1933).

Material examined.

†**S. pyramidatus*: Holotype and paratypes and many other lots (AMS).

S. crassiconus: Holotype (AIM) and 3 other lots (AMS).

Remarks. This genus is characterized by a conic to ovate-conic shell with the aperture separated from the parietal wall by a simple groove. It resembles some species of *Amphithalamus* in size but differs in the simple groove between the inner lip and the parietal wall and the spinose penis. The radular features also differ, the sharp primary cusps of the central and lateral teeth being in contrast with the broad, blunt cusps seen in *Amphithalamus* species. The lateral teeth are closer to those seen in species of *Rissoidea* than to other genera in the *Anabathrinae*.

Pseudestea contains a few species (mostly undescribed) found on the Continental Shelf and upper Continental Slope of southern and south-eastern Australia. *Scrobs crassiconus* Powell from northern New Zealand is (somewhat tentatively) referred here because of its similar shell.

Genus *Pisinna* Monterosato, 1878

Pisinna Monterosato, 1878:86. Type species *Rissoa punctulum* Philippi, 1836, by subsequent designation by Cossmann, 1921: 33. Recent, Mediterranean Sea (Figs 25F,G; 26F,G).

Hagenmulleria Bourguignat, 1881: 9. Type species *Hagenmulleria pechaudi* Bourguignat, 1881; here designated (= *Pisinna punctulum* (Philippi) *fide* Monterosato, 1894:114). Recent, Mediterranean Sea.

Estea Iredale, 1915: 451. Type species *Rissoa zosterophila* Webster, 1905; by original designation. Recent, New Zealand (Fig. 27A–D).

Nodulestea Iredale, 1955: 81. Type species *Estea castella* Laseron, 1950; by original designation. Recent, south-eastern Australia (Fig. 27G–I).

Feldestea Iredale, 1955: 81. Type species *Rissoa salebrosa* Frauenfeld, 1867; by original designation. Recent, south-eastern Australia (Fig. 27E,F).

? *Microstea* Ponder, 1965c: 156. Type species *Estea angustata* Powell, 1927; by original designation. Recent, northern New Zealand (Fig. 22G,H).

Diagnosis. *Shell*: Small to moderate size (1.2–3.8 mm in length), pupiform to elongate-ovate or ovate-conic, non-umbilicate. Aperture subcircular, with simple peristome; inner lip usually broad, attached to parietal wall; outer lip prosocline to opisthocline, with or without varix. Sculpture of axial or spiral ribs or both, or surface smooth (Figs 22G; 26F; 27C,E,G). Protoconch dome-shaped, of about $1\frac{1}{2}$ –2 whorls, surface minutely pitted, pits usually in close spiral rows (Figs 22H; 25G; 27A,F,H). Inner chitinous layer well developed.

Head-foot: Unpigmented or pigmented; cephalic tentacles paddle-shaped, snout bilobed; anterior mucous gland and propodium present; sole with long posterior mucous slit (Ponder, 1965c, 1968; Ponder & Yoo, 1976).

Anatomy: Female genital tract diaulic, spermathecal aperture at posterior end of pallial cavity (Fig. 7H,I,J). Penis simple, coiled, attached to midline of head (Fig. 8C).

Operculum: Simple, of 2 layers, oval, usually with low ridge just inside inner (columellar) edge. A weak projection just below nucleus in one species (*P. tropica* (Laseron), Ponder & Yoo, 1976, fig. 13e,f). Other species figured by Ponder (1965c) and Ponder & Yoo (1976) (Figs 26G, 27B).

Radula: Central teeth $\frac{3-1+1-3}{1}$, each with broad and blunt to narrow and sharp median cusp, basal denticles short; ventral edge more or less extended as a tongue-like structure in middle portion; lateral edges thickened, at 30°–40°. Lateral teeth 2–3 + 1 + 2–5, with cutting edge slightly longer than, or equal to, that of central teeth; primary cusp blunt to moderately sharp. Marginal teeth both simple, with several small, sharp cusps, those on inner marginal teeth slightly larger than those on outer marginal teeth; cutting edge of inner marginal teeth straight and at right angles to axis of tooth (Ponder & Yoo, 1976, figure the radula of several species) (Figs 25F; 27D,I).

Distribution. Mediterranean Sea, South Africa, Australia, New Zealand, tropical Western Pacific (see Ponder & Yoo, 1976).

Material examined.

†**P. punctulum*: Specimens ex Monterosato so named, ex Philippi (BMNH). Many other lots (AMS

and other museums).

†**R. zosterophila*: Paratypes and several other lots (AMS).

†**E. castella*: Types and many other lots (AMS).

†**E. salebrosa*: Types (NHMV) and many other lots (AMS).

**E. angustata*: Types (AIM) and a few other lots (NMNZ).

Many other species have also been examined.

Remarks. The species in this genus have been reviewed by Ponder (1965c) and Ponder & Yoo (1976). The radula, like the teleoconch sculpture, shows considerable diversity (Ponder & Yoo, 1976).

Pisinna appears to have had a southern origin (Ponder & Yoo, 1976) with the centre of speciation in New Zealand and temperate Australia. One of the species (*Barleia* [sic] *microthyra* Martens) included in *Pisinna* by Ponder & Yoo (1976) is a *Barleeia*.

Genus *Nodulus* Monterosato, 1878

Nodulus Monterosato, 1878:86. Type species *Rissoa contorta* Jeffreys, 1856; by subsequent designation by Bucquoy, Dautzenberg & Dollfus, 1884: 311. Recent, Mediterranean Sea (Fig. 26A–E).

Diagnosis. *Shell*: Minute (up to about 1.3 mm in length), solid, pupiform, non-umbilicate, with fine spiral sculpture, whorls convex, aperture broadly oval, with simple peristome, inner lip slightly separated from parietal wall; outer lip orthocline to weakly prosocline, non-varicose, with blunt edge (Fig. 25A). Protoconch of about $1\frac{1}{2}$ whorls, dome-shaped, sculptured with rather irregular pits, the surface between sometimes raised into weak, irregular wrinkles (Fig. 26B). Inner chitinous layer poorly developed.

Head-foot: Tentacles rather short, of even thickness, without obvious cilia or 'setae', held rather far to the sides of the head, showing little movement; eyes large. Foot short and slender, anterior corners forming right angles; posterior end simple, lanceolate. Snout bilobed, especially ventrally. No pallial or metapodial tentacles. Yellowish to brownish-greyish, very lightly coloured, with yellow spots behind eyes (Corsica; A Warén, *in. lit.*).

Operculum: Oval, flat, composed of two layers, paucispiral; inner surface with ridge along inner (columellar) edge and with two processes. One process rising from nucleus, subspiral, rather prominent, its distal portion vertical; other process small and vertical. Both connected by short, low, narrow ridge. Outer surface smooth except for radial growth lines (Fig. 26C,D).

Radula: Central teeth $\frac{3+1+3}{1}$, cusps sharp, primary cusp not conspicuously longer than adjacent cusps; each tooth with very small pair of processes high on outer edges of face; lateral thickenings rather weak, at about 30°; base with short, tongue-like process. Lateral teeth 2 + 1 + 2, with cutting edge narrower than that of central teeth, cusps sharp. Inner marginal teeth with longer cutting edge than lateral teeth, with

about 9 sharp cusps. Outer marginal teeth with smaller, sharp cusps (Fig. 26E).

Distribution. Mediterranean Sea (*R. contorta*).

Material examined.

†**R. contorta*: Probable syntypes (BMNH) and many other lots (several museums).

Remarks. This genus differs from others in the subfamily in the relatively large central teeth of the radula and in possessing two opercular pegs. In addition, the protoconch microsculpture, the lanceolate foot and the parallel-sided non-ciliated cephalic tentacles are also atypical. The presence of an opercular peg has resulted in this genus usually being classified with *Barleeia* by earlier authors. The general form of the operculum is, however, quite unlike that of *Barleeia* and is similar to that of some Anabathrinae, particularly in its possessing two discrete layers. The number of unique characters that *Nodulus* possesses suggests, however, that it has little close relationship with the other genera in the subfamily.

Discussion

Anatomy and Relationships: Convergence or Divergence?

Anatomically, as well as in shell characters, barleeids resemble rissoids and have long been included in the same family. Some of these resemblances are basic rissoacean characters (e.g. presence of a style sac containing a crystalline style, lack of an oesophageal gland, and the salivary glands or their ducts not passing through the circumoesophageal nerve ring). Other features shared with the Rissoidae, such as the closed pallial genital ducts and some shell characters, may either be due to convergence or be an indication of phyletic relationship. Some additional characters, which may be primitive, are shared with several rissoacean families and include the presence of metapodial and pallial tentacles (in *Fictonoba* and in many Rissoidae, Vitrinellidae, *Hydrobia* [Hydrobiidae] and some Iravadiidae), an opercular peg (also in *Rissoina* [Rissoidae], Cingulopsidae and Rastodentidae as well as the littorinacean Eatoniellidae), and the presence of an inner chitinous shell layer (also found in the Cingulopsidae and Eatoniellidae). The oesophageal pouches are almost certainly primitive, and are found in the Littorinidae (Fretter & Graham, 1962) and the Eatoniellidae (Ponder, 1968). Oesophageal pouches are possibly not present in the Cingulopsidae (although reported by Fretter & Patil, 1958), but in that family an oesophageal gland lies behind the nerve ring in some species (unpublished observations and Fig. 2D). The punctate or pitted protoconch microsculpture, so characteristic of the Barleeidae, is found in a few species of *Rissoina* but is otherwise rare in the Rissoidae (occurring in only four other genera). A shallow pitted protoconch microsculpture is typical of the Hydrobiidae but most other rissoacean families lack such sculpture.

An inner chitinous shell layer, a pegged operculum and a minute, conical, simple shell are found in the littorinacean Eatoniellidae (Ponder, 1965a; Ponder & Yoo, 1978) and the rissoacean Cingulopsidae (Ponder & Yoo, 1980) and Rastodentidae (Ponder, 1966), as well as the Barleeidae. The barleeids differ from the above families in being phallate. These families may form a closely related group which evolved separately from the rest of the Rissoacea from an eatoniellid-like ancestor. Further work is required to establish whether or not this is the case. A major problem with such a scenario is the similarity between *Fictonoba* and the rissoids, especially *Rissoina*. Given the number of characters in common, it is possible that *Rissoina* and *Fictonoba* are related and that the Rissoidae (i.e. a *Rissoina*-like ancestor) evolved from a *Fictonoba*-like barleeid. This question was also addressed in the discussion on *Fictonoba* where it was suggested that the resemblances between *Fictonoba* and the Rissoidae may also be due to convergence.

The evolutionary relationships of most of the families mentioned in the Discussion are summarized in Fig. 9.

The Radula

The central teeth of the radula of species of Barleeinae have, with the exception of *Caelatura*, a U-shaped projection on their lower face which abuts against the upper edge of the tooth in front, probably preventing it from sliding forwards when pressure is applied during scraping. The ventral margin extends beneath the tooth in front where it fits into a shallow socket behind the upper part of the tooth. This arrangement would prevent the base of the tooth from tipping forwards and, perhaps, tearing loose from the basement membrane during scraping.

In *Caelatura* the U-shaped projection is absent but the basal denticles overlap the teeth in front and probably serve the same purpose. The basal denticles in the other genera do not appear to be in a position to function in this way and their role is obscure. Species of the Anabathrinae have no U-shaped basal projection and the basal denticles do not overlap the tooth in front. Whereas it seems probable that these different radular structures are related to different feeding strategies, the gut contents of all the species examined anatomically were similar, consisting of diatoms, algal cells and some detrital material. Differences may occur in the amount of force exerted by the radula while scraping the substratum enabling subtly different types of grazing to occur.

The Oesophageal Pouches

The oesophageal pouches of *Barleeia* resemble an oesophageal gland and appear to be an anterior extension of that gland. Similar structures are found in *Lacuna* sp. (Fretter *in lit.*) *Littorina* spp. (Fig. 2C) (Fretter & Graham, 1962), and *Laevilitorina mariae* (T. Woods) (my own observations) (Fig. 2B). In these species the anterior oesophagus narrows considerably through the nerve ring with a consequent disappearance

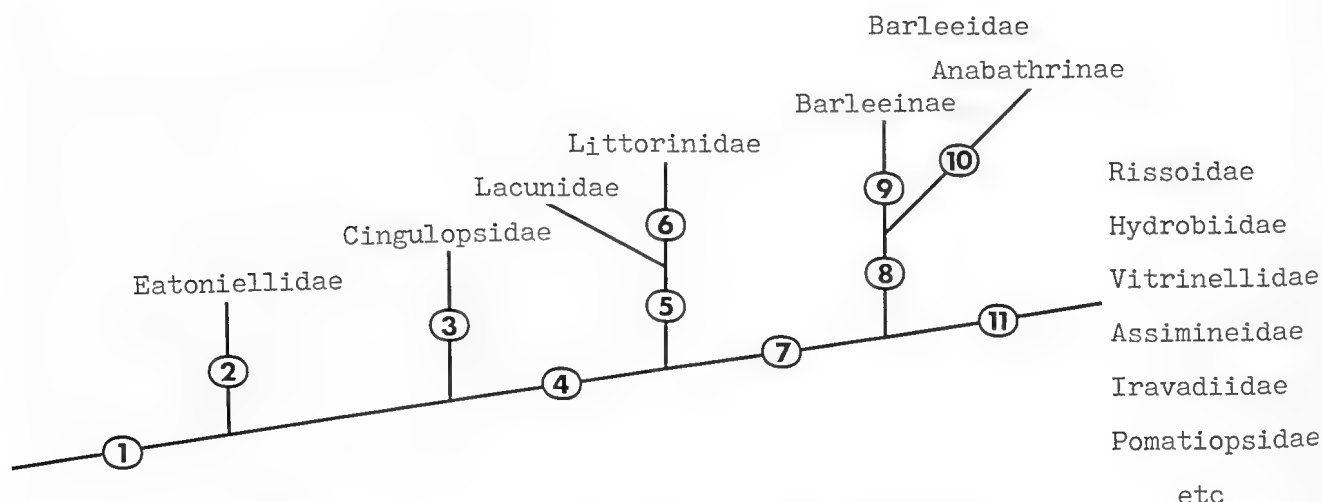


Fig. 9. Diagrammatic representation of the possible relationships of some of the littorinean and rissocean families. Numbers in the diagrams represent the presence of the following characters and states.

1. Inner chitinous shell layer; opercular peg; salivary glands/ducts pass through the nerve ring; oesophageal gland and pouches present; style sac but no crystalline style; male and female pallial genital ducts open; aphallate, with posterior sac for sperm storage (seminal receptacle); larval development pelagic; tentacles on opercular lobe present; posterior pedal gland present with long, slit-like opening reaching to posterior end of foot.
2. Direct development; development of pallial sperm-receiving structure in some; posterior pallial tentacle in one genus.
3. Closure of pallial genital duct and development of visceral bursa copulatrix; oesophageal gland lost in some species; style sac lost; loss of accessory tentacles.
4. Penis developed.
5. Loss of inner chitinous shell layer; loss of opercular peg; partial or complete closure of pallial genital ducts; tendency to coiling of oviduct glands; development of anterior bursa copulatrix; loss of slit-like posterior pedal gland opening.
6. Loss of tentacles on opercular lobe.
7. Development of crystalline style; salivary glands/ducts do not pass through nerve ring; development of secondary sperm storage (usually a bursa copulatrix derived from sperm groove); development of metapodial and pallial tentacles; loss of opercular lobe tentacles.
8. Loss of oesophageal gland; complete closure of male and female pallial genital ducts; direct development.
9. Loss of metapodial and pallial tentacles in all but one genus.
10. Partial or complete loss of opercular peg; loss of oesophageal pouches, operculum two-layered, loss of metapodial and pallial tentacles.
11. Loss of inner chitinous shell layer, oesophageal gland and oesophageal pouches; posterior pedal gland lost or, in some, present with small opening in middle of metapodial sole.

of the glandular epithelium of the oesophageal gland and the oesophageal gland proper lies behind the nerve ring. In the most primitive state, as seen in some species of *Eatoniella* (Eatonellidae) and *Macquariella kingensis* (May) (Littorinidae), the glandular epithelium of the oesophageal gland passes through the nerve ring and is continuous with that of the oesophageal pouches (Fig. 2A). The oesophageal pouches seen in *Barleeia* (Fig. 2G) are histologically and morphologically so similar to those of the Littorinidae that they are almost certainly homologous. It appears that the oesophageal pouches in the Littorinacea and the Barleeidae are an anterior remnant of the oesophageal gland.

Both the oesophageal gland and the oesophageal pouches are lost in *Fictonoba*, as well as in the Anabathrinae, although this subfamily has well-developed dorsal folds in the oesophagus. The Cingulopsidae have apparently lost the oesophageal pouches but some have an oesophageal gland (Fig. 2D),

although this is lost in at least one species—*Skenella* (= *Eatoniopsis*) *castanea* (Laseron) (Fig. 2E).

The salivary glands pass through the nerve ring in the majority of mesogastropods and this state is observed in the littorinean families Eatonellidae (Fig. 2A) and Littorinidae (Fig. 2A–C) and in the rissocean family Cingulopsidae (Fig. 2D,E). The other rissocean families have the salivary glands placed above the nerve ring (Fig. 2F,G), this presumably being a derived state.

Ponder (1973) considered the oesophageal pouches of *Littorina* to be homologous with the buccal pouches seen in some Archaeogastropoda. If the oesophageal pouches are derived from the oesophageal gland they are clearly not homologous.

The Female Genital System

The female genitalia of the Barleeidae can be derived from an ancestral state having an open, pallial capsule

gland with a sperm groove along the ventral edge of the left (inner) side (Fig. 5A,B). This gland would have been continuous with the albumen gland, which lies behind the posterior pallial wall, displacing the kidney. A posterior seminal receptacle on the left side of the albumen gland probably opened adjacent to the short, renal oviduct, into the ventral wall of the anterior end of the albumen gland.

Of all the species examined *Lirobarleeia galapagensis* (Fig. 5C,D) is the most similar to this basic type. The capsule gland is closed and the sperm groove is contained within the ventral channel formed from the fusion of the two ventral edges of the walls of the capsule gland. This sperm groove has been nipped off to form a spermathecal tube in *Fictonoba carnosus* (Fig. 5E,F), *Anabathron contabulatum* (Fig. 7C,D) and *Badepigrus pupoides* (Fig. 7A,B), but it maintains communication with the anteriorly placed vestibule in all these species. In *Barleeia* spp. (Fig. 5G,H), *Pisinna* spp. (Fig. 7H-J) and *Amphithalamus incidatus* (Fig. 7E-G) the spermatheca has severed its connection with the anterior oviduct and opens in the posterior part of the pallial cavity. In *Pisinna* and *Barleeia* this opening is at the posterior end of the pallial cavity but in *A. incidatus* it is placed more anteriorly. It is highly probable, given their dissimilarity in many other characters, that the diaulic condition in *Pisinna* and *Barleeia* was independently derived. Similar short spermathecal ducts with an independent opening are found in the Pomatiopsidae (Davis, 1979, 1980), the Stenothyridae (Kosuge, 1969), the Cingulopsidae (Fretter & Patil, 1958) and the Hydrococcidae (in which the bursa opens directly to the exterior) (Ponder, 1982).

An alternative derivation of the posterior spermathecal opening in *Barleeia* is that the ventral walls of the capsule gland may have sealed in the middle section, leaving a posterior and an anterior opening. This explanation is, in my view, much less likely than the loss of the pallial part of the spermathecal tube. The ventral fusion of the walls of the capsule gland in those species with a separate spermathecal opening is more complete than in *Lirobarleeia* and *Fictonoba*, and has resulted in a central lumen in *Barleeia*.

The sperm groove in *Lirobarleeia* appears to be enlarged posteriorly to store sperm (Fig. 5C,D: sz) and is thus analogous to that of *Iravadia* (*Pseudomerelina*) *mahimensis* (Melvill) (Ponder, 1984). In the Iravadiidae this sperm groove appears to have moved dorsally to provide a greater storage area in some species. A parallel situation appears to have occurred in the Barleeidae. *Fictonoba* (Barleeinae) has a bursal sac placed dorsally between the capsule and albumen glands and similar sacs occur in all species of Anabathrinae studied. Species of *Barleeia* do not have a bursa copulatrix but have developed a sperm storage area in a lobe of the albumen gland.

The seminal receptacle was in the same position in all the species studied and shows little modification.

The fertilization area is unmodified in *Fictonoba*, where it is simply the ventral anterior portion of the

albumen gland. The histology of this area is markedly modified in *Lirobarleeia* and *Barleeia* but it is widely open to the albumen gland. In the Anabathrinae it is a separate structure, presumably budded off from the albumen gland. It is tubular in some and a simple cavity in others. The area anterior to the fertilization chamber is a narrow tube lined with large, cuboidal, pale-blue-staining cells in all species of Anabathrinae except those in *Pisinna*. Those species have lost the tube because of their posterior spermathecal opening.

The renal section of the oviduct is short and simple in *Pisinna* and in the Barleeinae but has developed into a U-shaped loop in the other species of the Anabathrinae investigated. In these the U-shaped tube lies ventrally along the albumen gland and is narrow throughout. It is analogous to the coiled oviduct of the Hydrobiidae and the upper oviduct of the Rissoidae but is almost certainly independently derived.

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Table 1. Character states of some important characters in the Rissoidae and Barleeidae (+, present; -, absent; (+), rarely present; (-), rarely absent. Characters have been selected that show differences between the groups under consideration. Characters or states present only in the atypical barleeid genus *Fictonoba* are in parentheses and marked with an asterisk in the Barleeinae column.

	Rissoidae	Barleeidae	
		Barleeinae	Anabathrinae
<i>Shell</i>			
With inner chitinous layer	-	+	+
With punctate protoconch	- (+)	+	+
<i>Operculum</i>			
With peg on inner surface	- (+)	+	- (+)
With prominent longitudinal ridge on middle of inner surface	-	+	-
Composed of two layers	-	-	+
<i>Radula</i>			
Cusps on outer edge of outer marginal teeth	- (+)	+	-
<i>Head-foot</i>			
Metapodial tentacle(s) present	+ -	- (+)*	-
Pallial tentacle(s) present	+ -	- (+)*	-
Cephalic tentacles long and slender	+	+	-
Posterior pedal gland opening (when present) extends to posterior end of foot	-	+	+
<i>Anatomy</i>			
Jaws present	+	+ -	+ -
Buccal pouches present	-	+ (-)*	-
Dorsal folds in mid-oesophagus long	-	-	+
Spermathecal duct opens to posterior end of pallial cavity	-	+ -	- (+)
Oviduct with two separate glands	+	-	-
Lower oviduct gland (capsule gland) with ventral sperm gutter	+ (-)	- (+)	-
Bursa copulatrix (when present) on left side of albumen gland	-	+	+
Seminal receptacle on left side of albumen gland	-	+ (-)*	+

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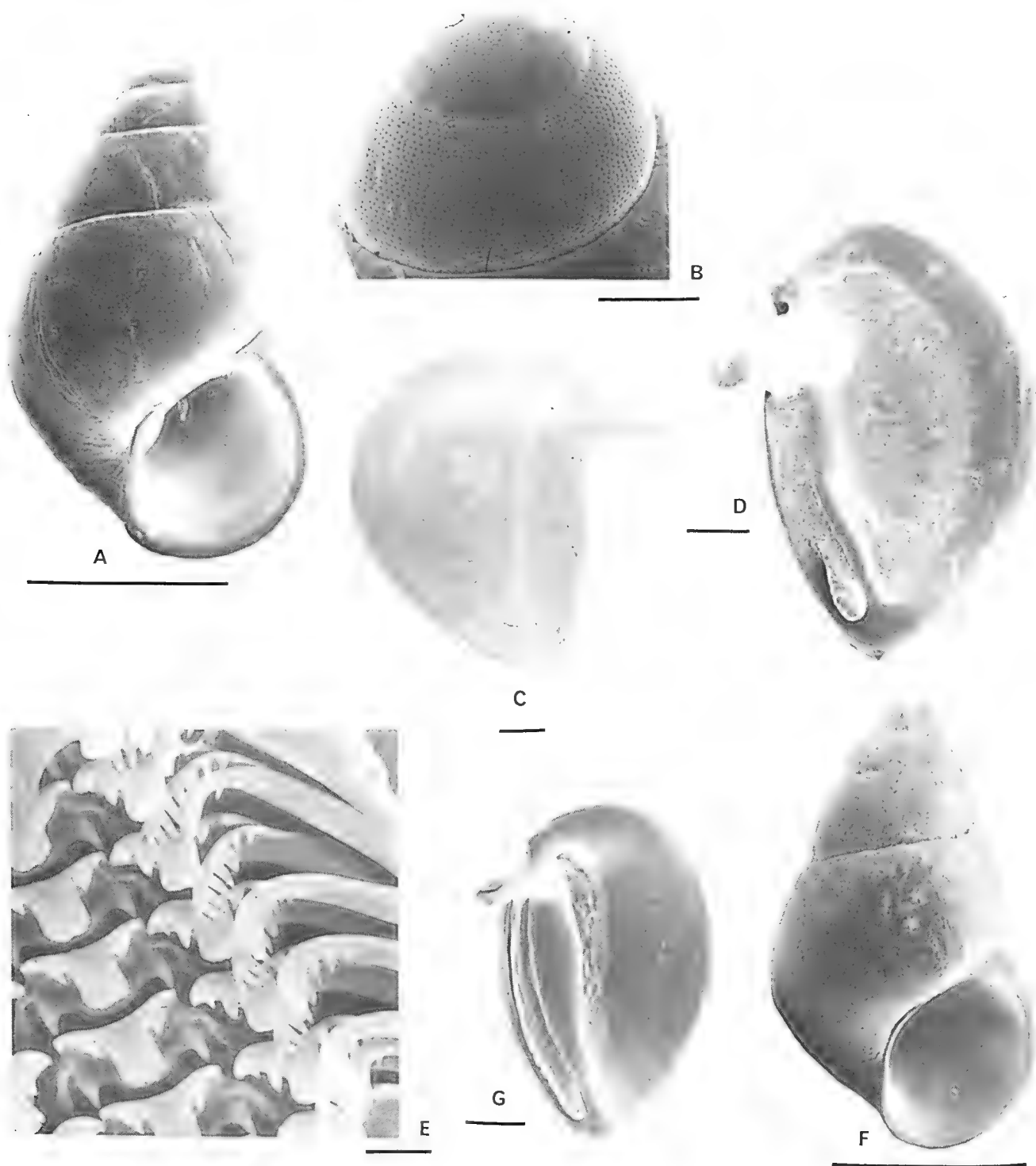


Fig. 10. A-E, *Barleeia unifasciata* (Montagu), type species of *Barleeia* Clark: A, shell; B, protoconch; C & D, operculum (C, outer side, D, inner side); E, radula. (A-D, Wembury, England, AMS C. 137204; E, Devon, England, NMV F26633). F & G, *Barleeia angustata* (Pilsbry), type species of *Ansola* Slavoshevskaya; Posyet Bay, USSR, AMS C.139454.

Scales: shells—1 mm; protoconch and opercula—0.1 mm; radula—0.01 mm.

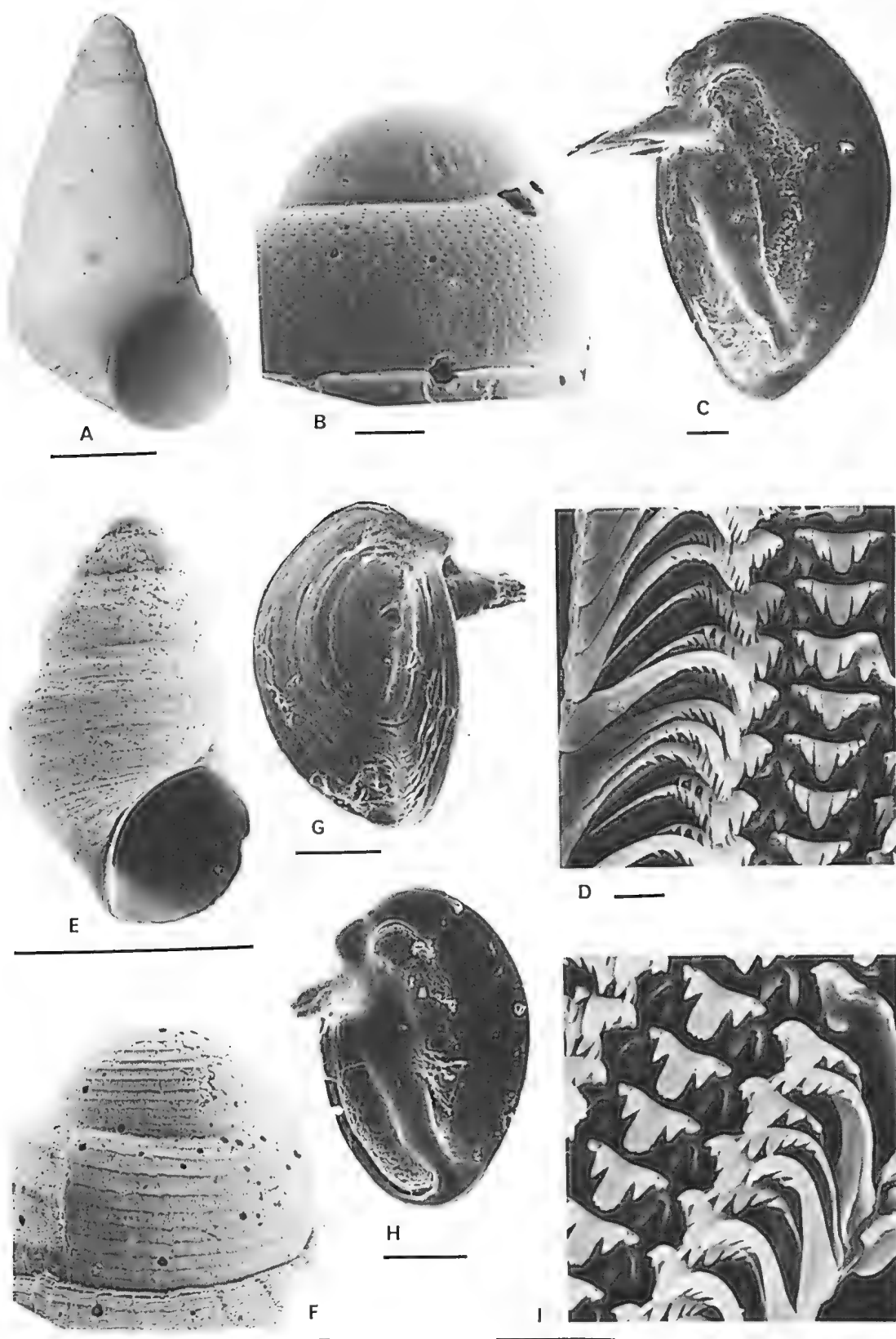


Fig. 11. A-D, *Barleeia acuta* (Carpenter), type species of *Pseudodiala* Ponder: A, shell; B, protoconch; C, operculum (inner side); D, radula (Franklin Point, San Mateo County, California, AMS C.137205, ex LACM 62-8). E-I, *Protobarleeia myersi* (Ladd), type species of *Protobarleeia* n.gen.: E, shell; F, protoconch; G & H, operculum (G, outer side, H, inner side); I, radula (Wilson Island, Capricorn Group, Queensland, Australia, AMS C. 137469). Scales: shells—1 mm; protoconchs and opercula—0.1 mm; radulae—0.01 mm.

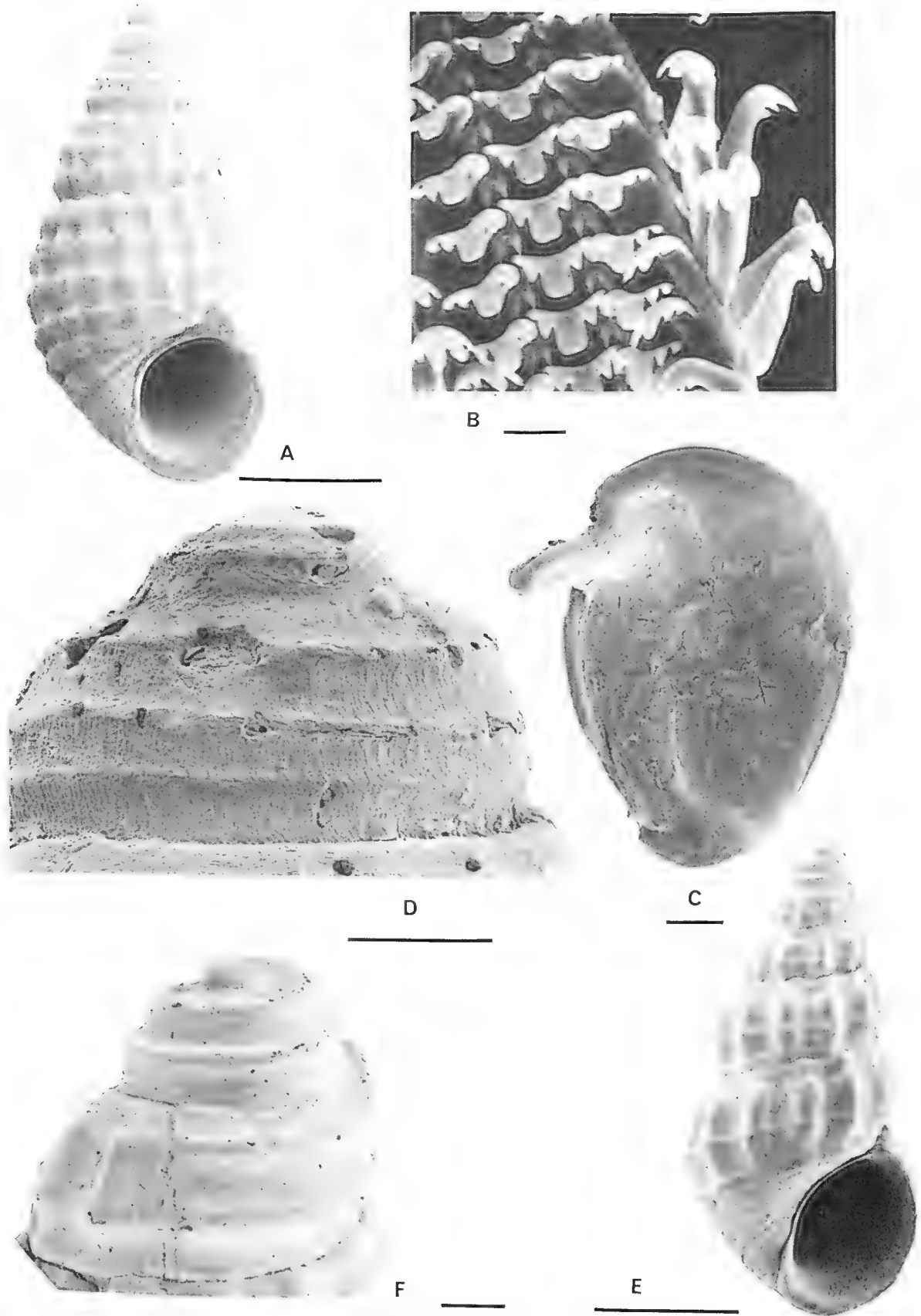


Fig. 12. A–D, *Lirobarleeia galapagensis* (Bartsch), type species of *Lirobarleeia* n.gen: A, shell; B, radula; C, operculum (inner side); D, protoconch (A, C, D, Bahia Academy, Isla Santa Cruz, Galapagos Islands, 0–12 m, AMS C.137206, ex LACM 66-120; B, between Pta Tomayo and Bahia Academy, 0–2 m, AMS C.137207, ex LACM 66-119). E, F, *Lirobarleeia nemo* (Bartsch): E, shell; F, protoconch (Gardner Bay, Hood Island, Galapagos Islands, 64 m, AMS C. 137208, ex LACM, AHF 453).

Scales: shells—1 mm; protoconchs and operculum—0.1 mm; radula—0.01 mm.

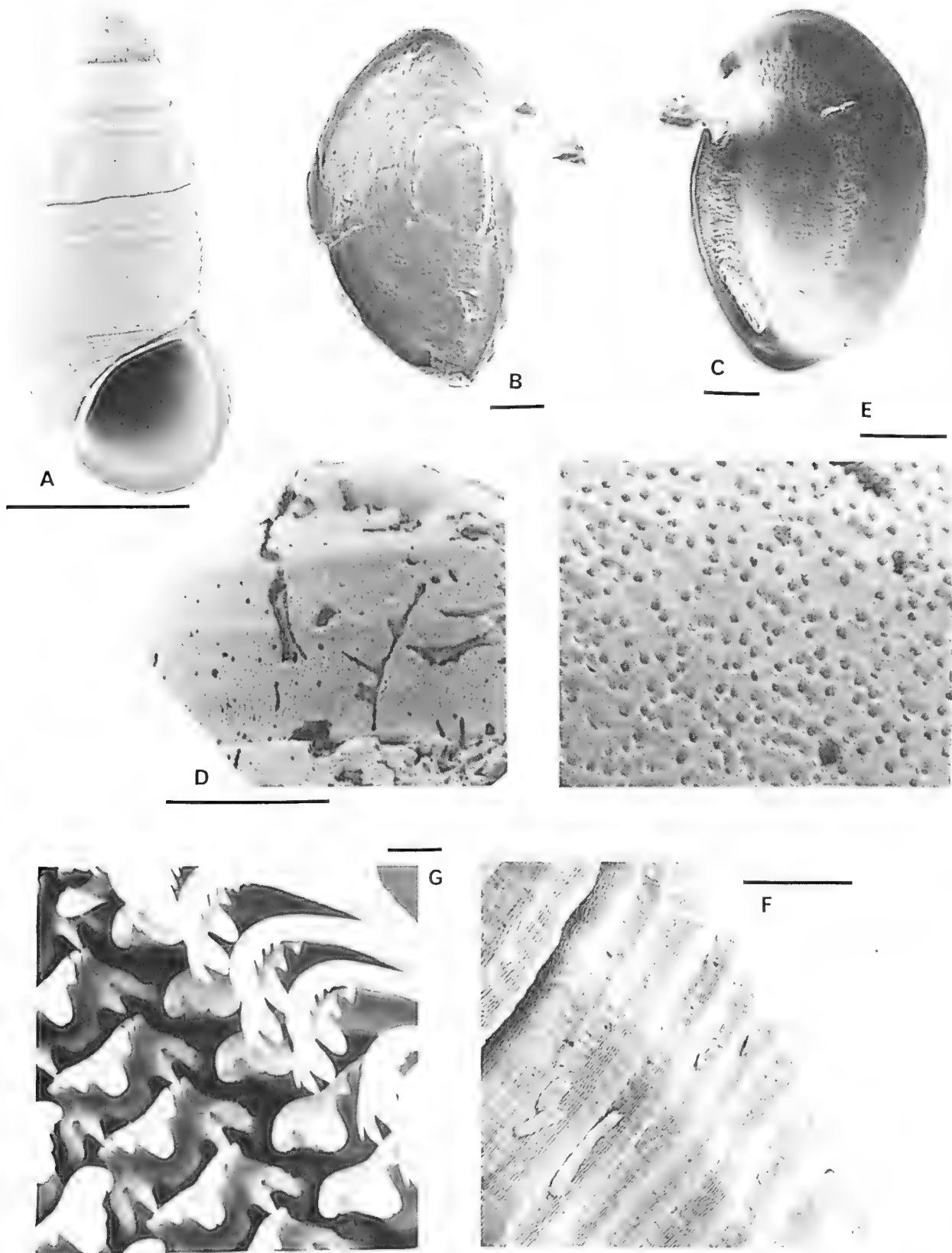


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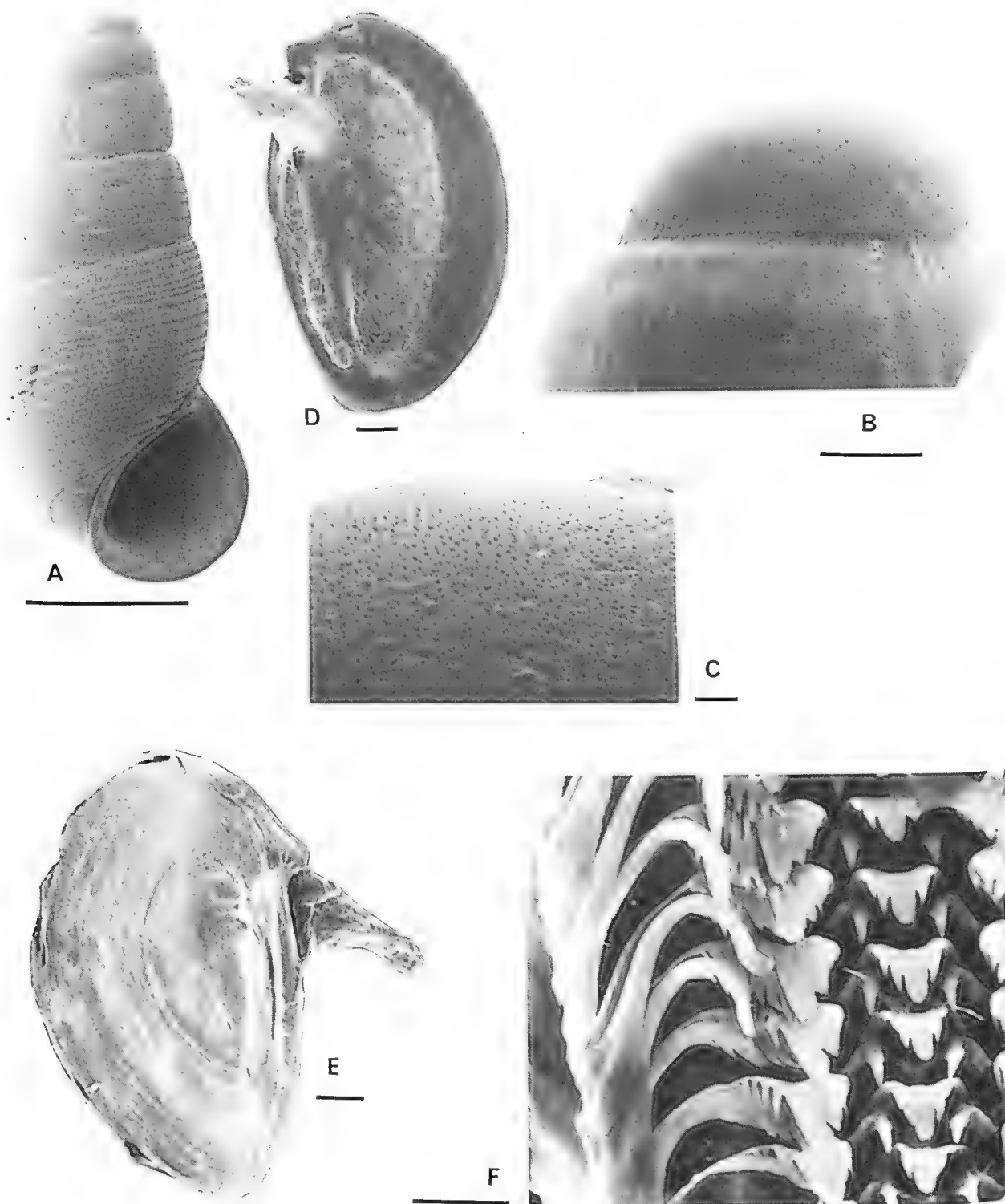


Fig. 14. *Lirobarleeia kelseyi* (Dall & Bartsch): A, shell; B & C, protoconch (C, microsculpture); D & E, operculum (D, inner side, E, outer side); F, radula (South Anchorage, Guadalupe Island, Baja California, Mexico, 15–37 m, AMS C.137210 ex LACM 65–42).

Scales: shell—1 mm; protoconch and opercula—0.1 mm; microsculpture and radula—0.01 mm.

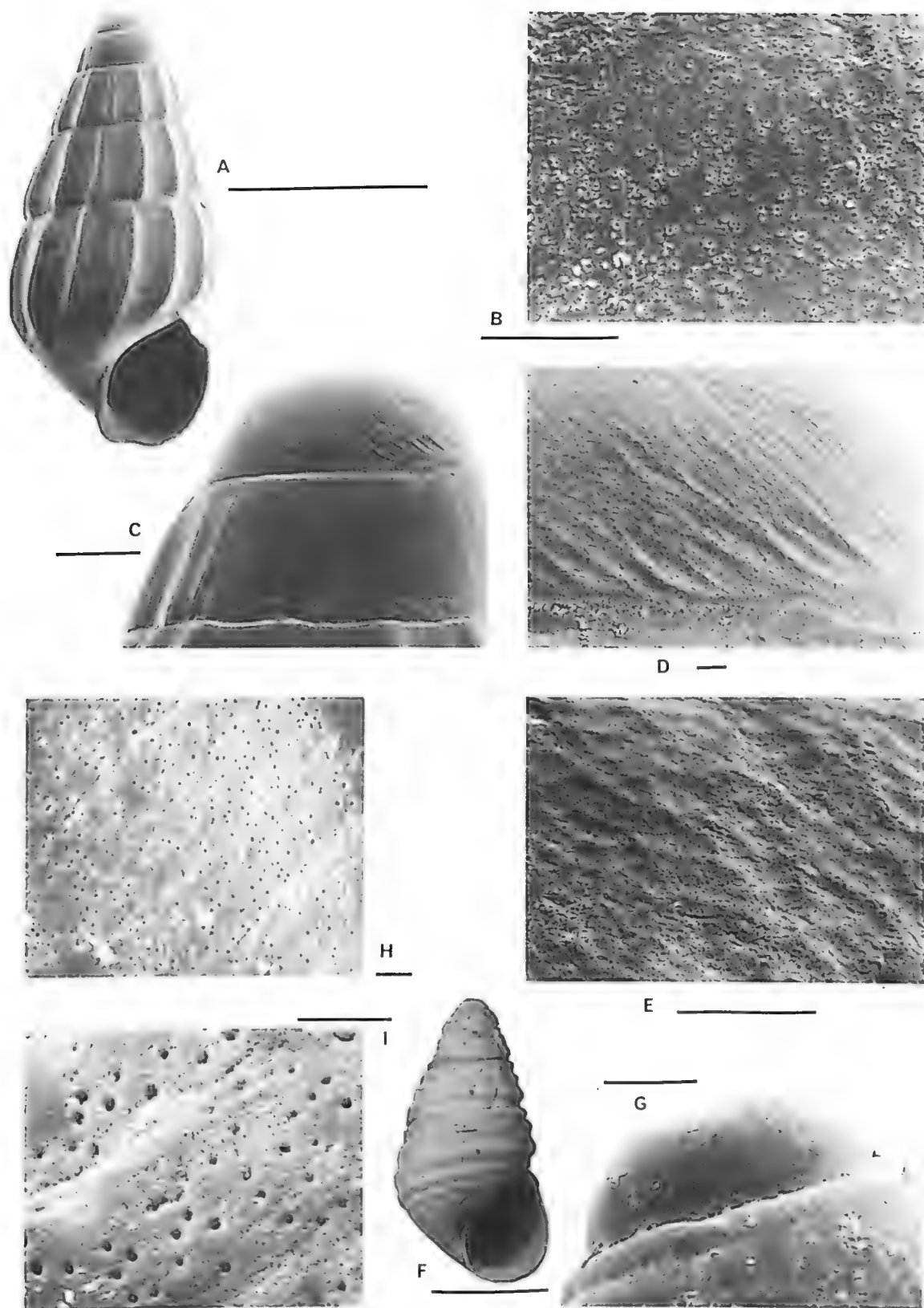


Fig. 15. A-E, *Caelatura microstoma* Watson: A, shell (subadult); B, teleoconch microsculpture; C-E, protoconch (D & E, microsculpture) (146-339 m, off Pta Jiguero, Puerto Rico, USNM 430681). F-I, *Caelatura sulcata* (Lea), type species of *Caelatura* Conrad: F, shell; G, protoconch; H & I, teleoconch microsculpture (Claiborne, Alabama, USA, Eocene, ANSP 10039). Scales: shells—1 mm; protoconchs, and microsculpture figure H—0.1 mm; microsculpture figures B,D,E,I—0.01 mm.

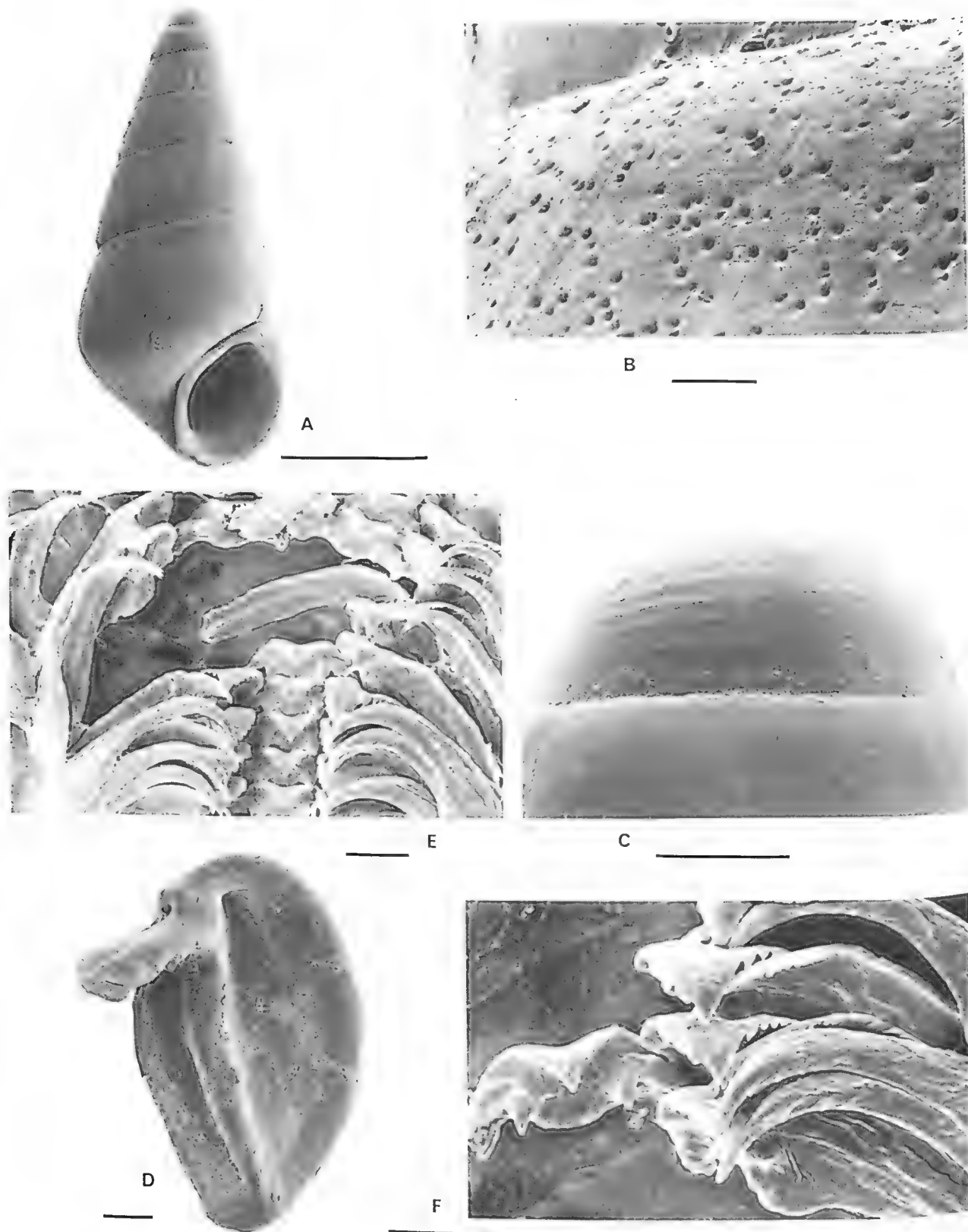


Fig. 16. *Caelatura rustica* (Watson): A, shell; B, teleoconch microsculpture, C, protoconch; D, operculum (inner side); E & F, radula (F, detail of central tooth) (syntypes of *Alaba conoidea* Dall, Campeche Bank, Gulf of Mexico, 377 m, USNM 94287).

Scales: shell—1 mm; protoconch and operculum—0.1 mm; microsculpture and radulae—0.01 mm.

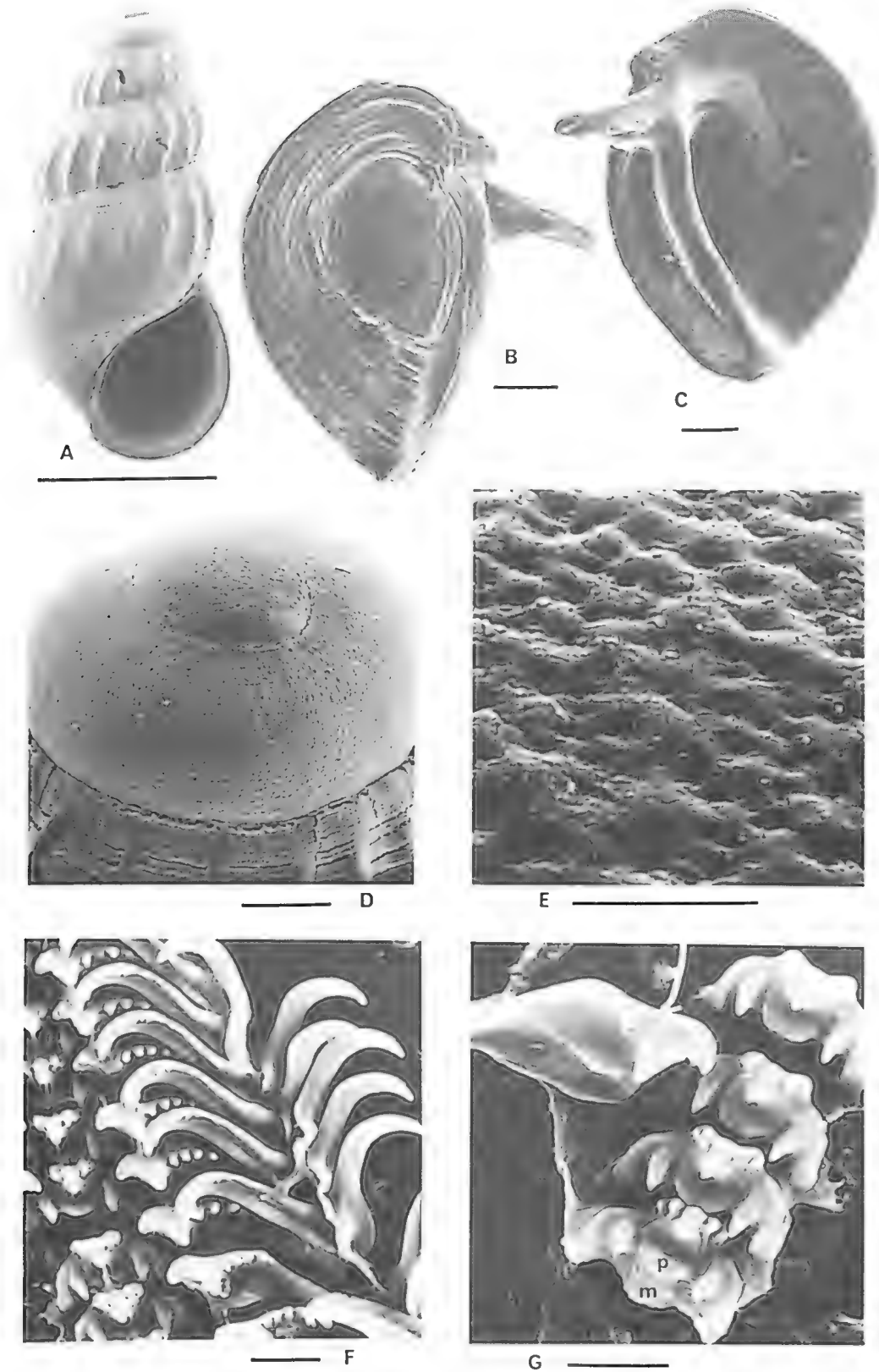


Fig. 17. *Ficonoba carnosa* (Webster), type species of *Ficonoba* Ponder: A, shell; B & C, operculum (B, outer side, C, inner side); D & E, protoconch (E, microsculpture); F & G, radula (G, detail of central teeth) (Taurikura Bay, Whangarei Heads, Northland, New Zealand, AMS C.137470). *p*, U-shaped projection on face of central tooth; *m*, ventral margin of central tooth.

Scales: shell—1 mm; protoconch and opercula—0.1 mm; microsculpture and radulae—0.01 mm.

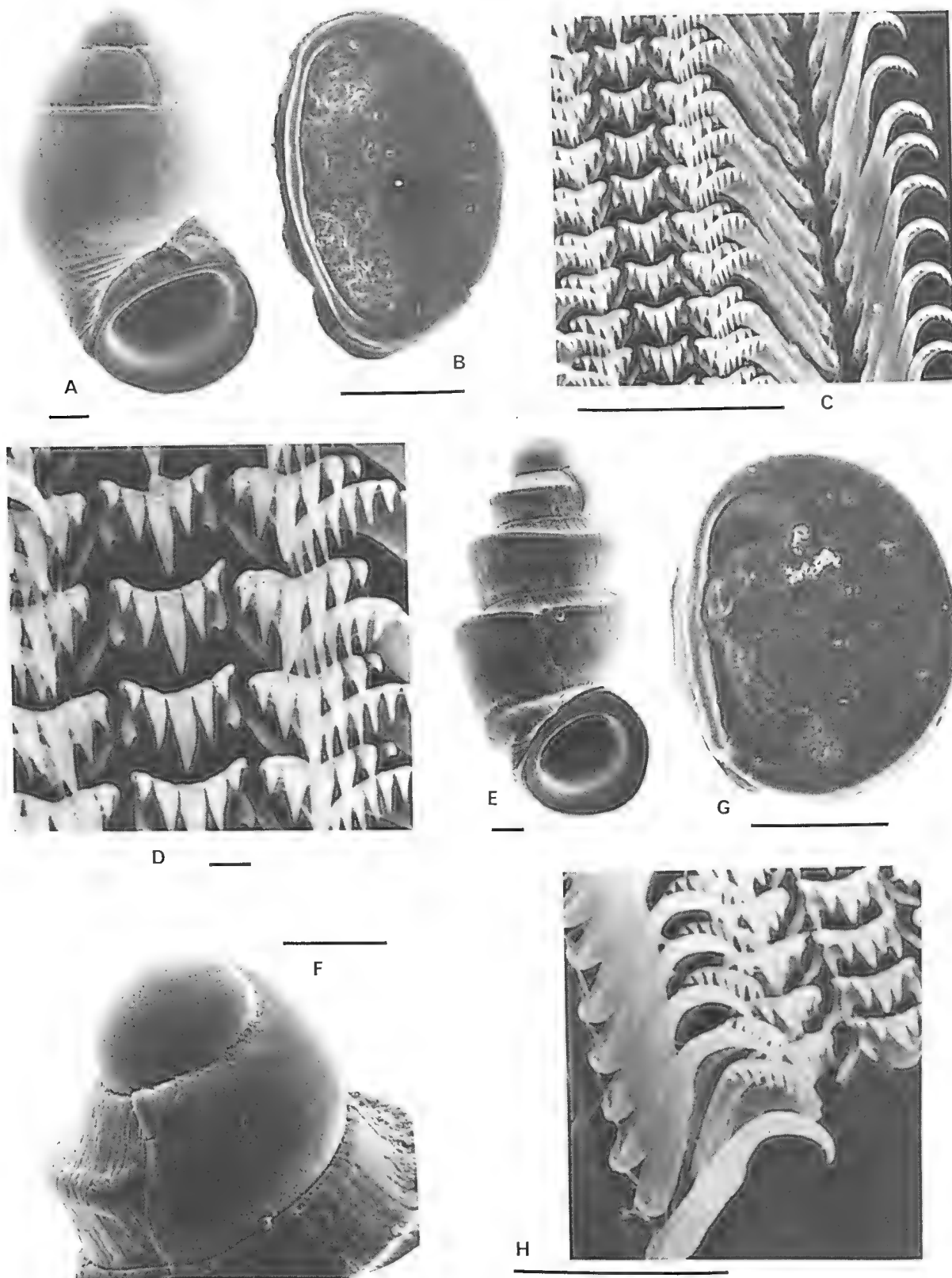


Fig. 18. A-D, *Anabathron (Scrobs) luteofuscus* (May): A, shell; B, operculum (inner side); C & D, radula (D, detail of central teeth) (Long Reef, Collaroy, NSW, AMS, C.139453). E-H, *Anabathron (Anabathron) contabulatum* (Frauenfeld); type species of *Anabathron* Frauenfeld: E, shell; F, protoconch; G, operculum (inner side); H, radula (E & H, Forster, NSW, AMS C.73159; F, G, Long Reef, Collaroy, NSW, AMS C.137211, C.137471). Scales: shells, protoconch and opercula—0.1 mm; radulae figures C and H—0.01 mm; radula figure D—0.001 mm.

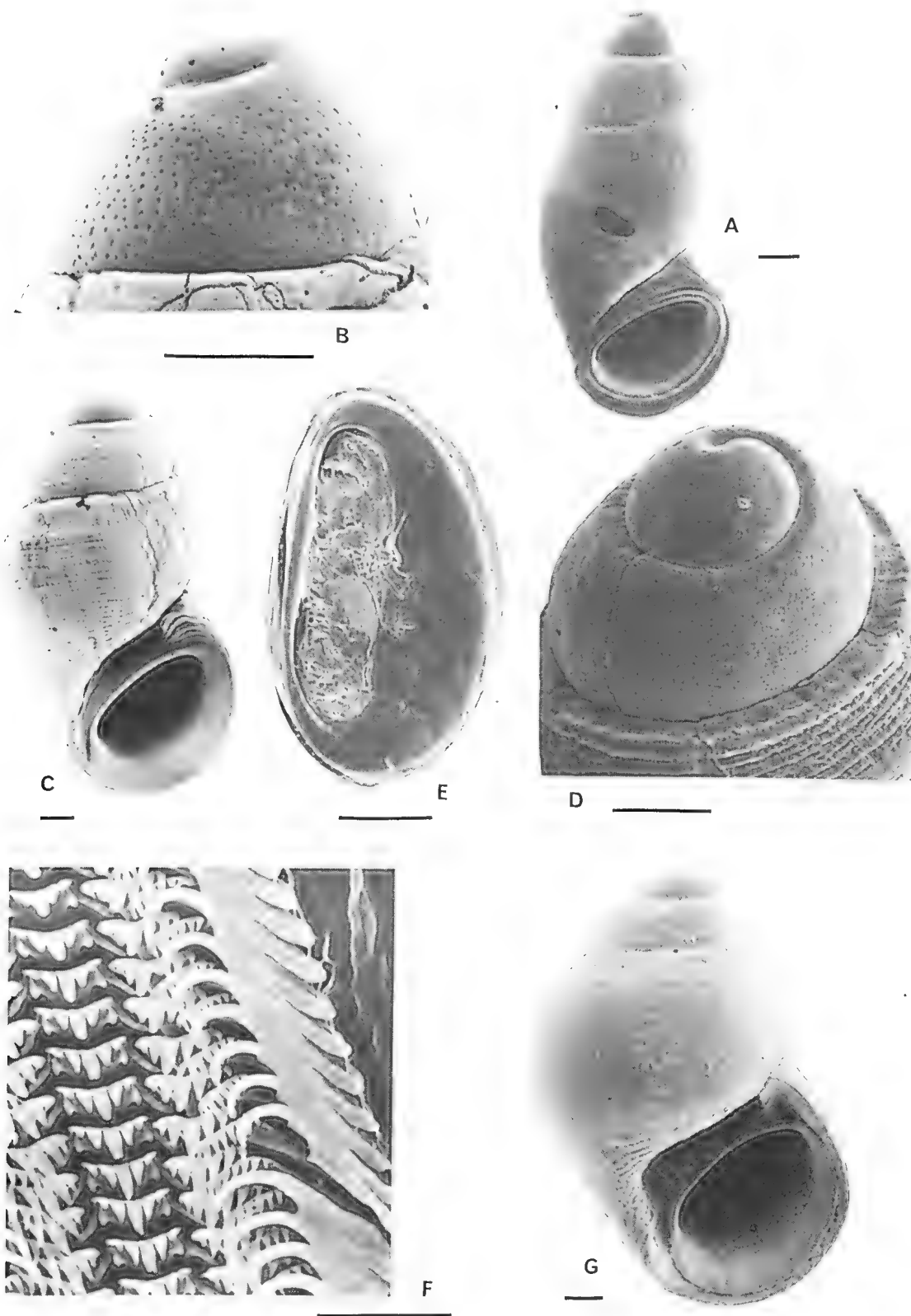


Fig. 19. A & B, *Anabathron (Scrobs) scrobiculator* (Watson), type species of *Scrobs* Watson: A, shell; B, protoconch (Ocean Beach, Manly, NSW, AMS C. 137472). C–F, *Anabathron (Scrobs) hedleyi* (Suter), type species of *Nannoscrobs* Finlay: C, shell; D, protoconch; E, operculum (inner side); F, radula (W side, Lyall Bay, Wellington, New Zealand, AMS C.137212). G, *Anabathron (Scrobs) pluteus* (Laseron), type species of *Ultisrobs* Iredale: shell (syntype, Sow and Pigs Reef, Sydney, NSW, 10–16 m, AMS C. 102489). Scales: shells, protoconchs, and operculum—0.1 mm; radula—0.01 mm.

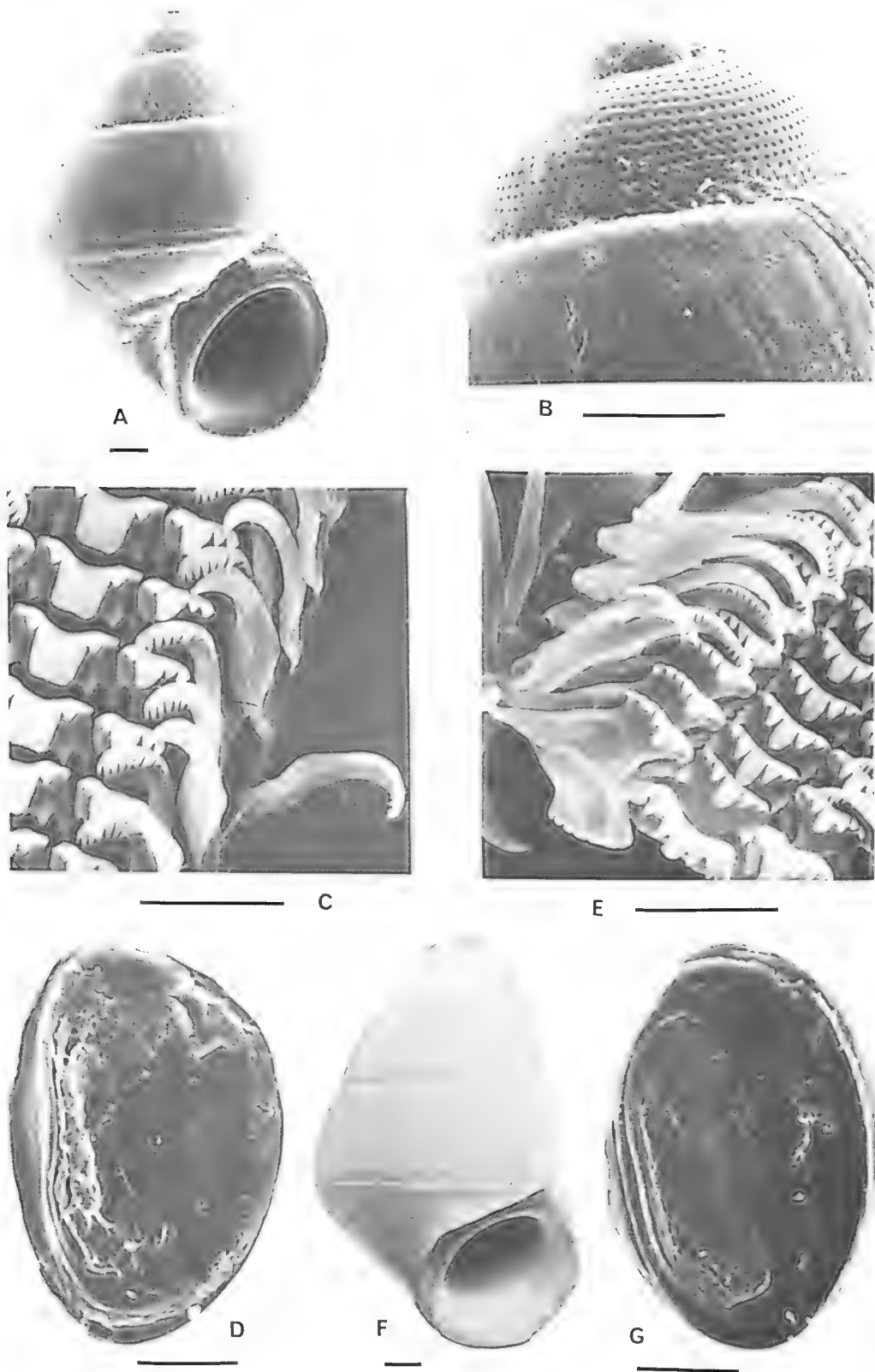


Fig. 20. A-D, *Amphithalamus* (*Amphithalamus*) *inclusus* Carpenter, type species of *Amphithalamus* Carpenter: A, shell; B, protoconch; C, radula; D, operculum (inner side) (Wilson Cove, San Clemente Island, Los Angeles County, California, AMS C.137213, ex LACM 66-51). E-G, *Amphithalamus* (*Amphithalamus*) *incidatus* (Frauenfeld), type species of *Microfossa* Laseyron: E, radula; F, shell; G, operculum (inner side) (F, Shelly Beach, Manly, NSW, AMS C.137455; E & G, Forster, NSW, AMS C.73202). Scales: shells, protoconch and opercula—0.1 mm; radulae—0.01 mm.

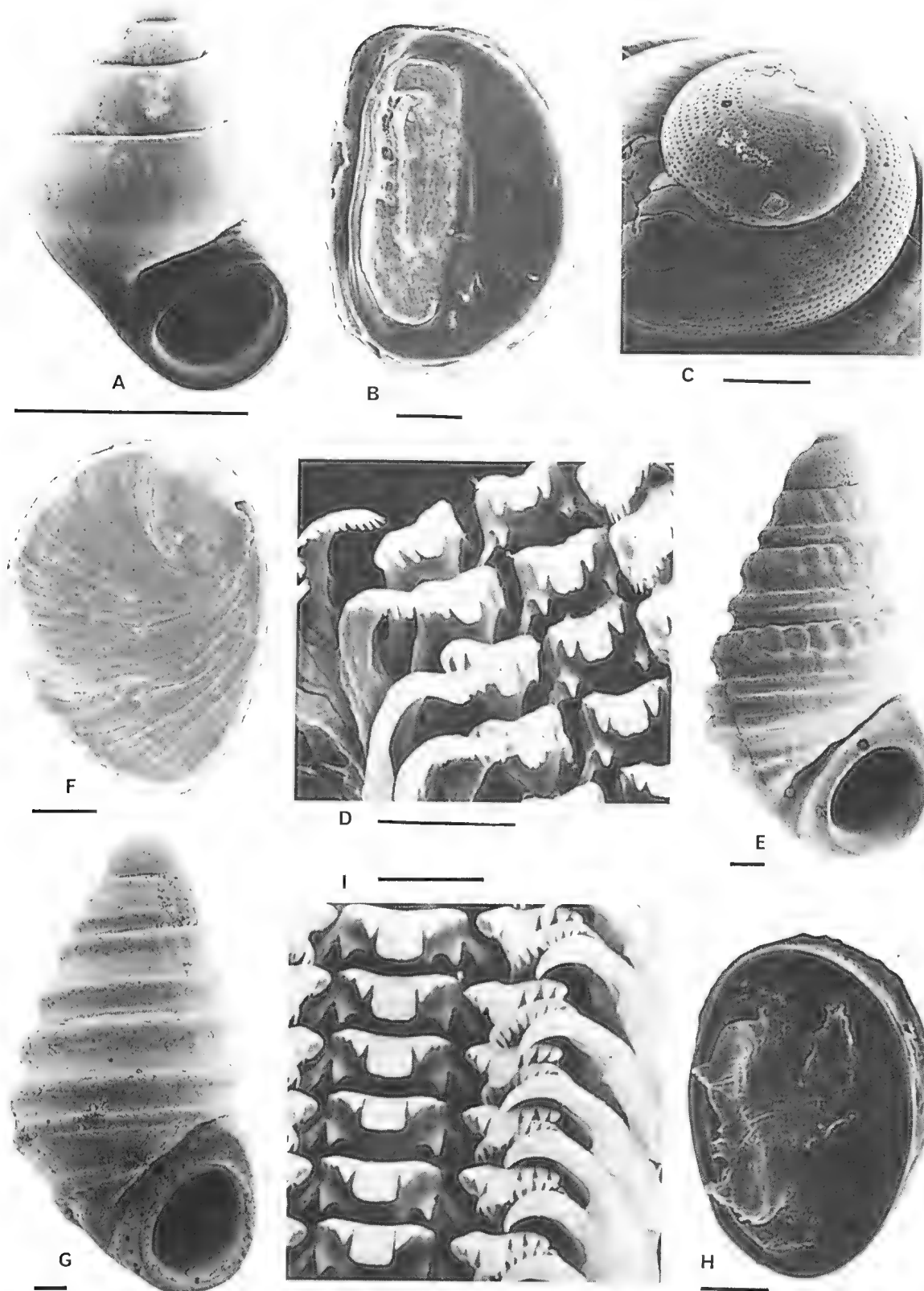


Fig. 21. A–D, *Amphithalamus* (*Amphithalamus*) *jacksoni* (Brazier), type species of *Obescrobs* Iredale: A, shell; B, operculum (inner side); C, protoconch; D, radula (Balmoral, Middle Harbour, Sydney, NSW, 18 m, AMS C.137456). E, *Amphithalamus* (*Notoscrops*) *ornatus* (Powell), type species of *Notoscrops* Powell: shell (Tapeka Point, Russell, Bay of Islands, New Zealand, AMS C.137457). F–I, *Amphithalamus* (*Notoscrops*) *liratus* Thiele: F & H, operculum, (F, outer side, H, inner side); G, shell; I, radula (Dunsborough, southern Western Australia, AMS C.137474). Scales: shell A–1 mm; shells E & G, protoconchs and opercula—0.1 mm; radulae—0.01 mm.

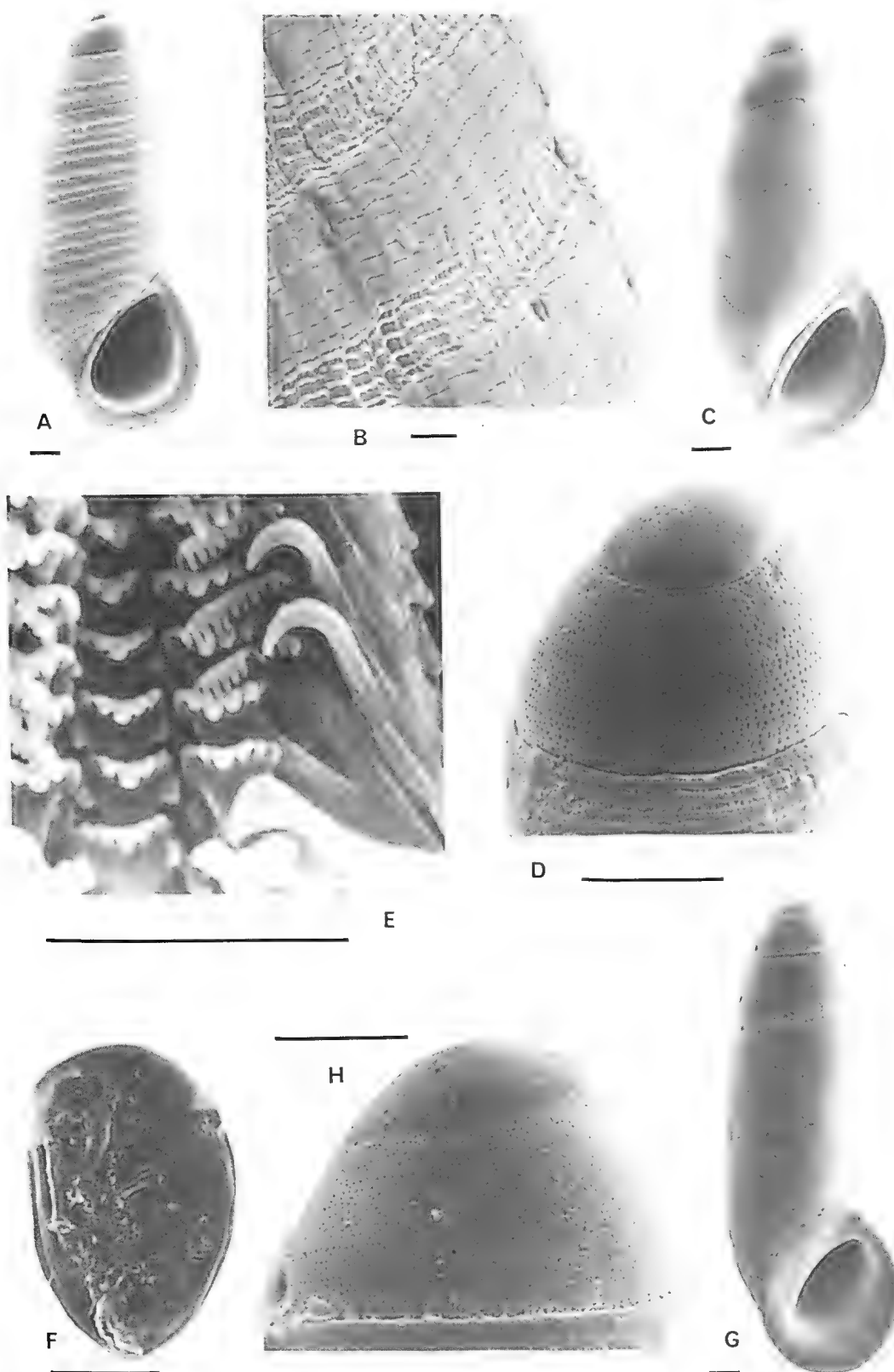


Fig. 22. A & B, *Microdryas iravadioides* (Gatliff & Gabriel), type species of *Microdryas* Lasezon: A, shell; B, teleoconch microsculpture (off Sow and Pigs Reef, Sydney, NSW, AMS C.137458). C-F, *Microdryas* sp.: C, shell, D, protoconch; E, radula; F, operculum (inner side) (Lord Howe Island, AMS C.59742). G & H, *Pisinna angustata* (Powell), type species of *Microstema* Ponder: G, shell; H, protoconch (Spirits Bay, Northland, New Zealand, NMNZ M.20375).

Scales: shells, protoconch and operculum—0.1 mm; microsculpture and radula—0.01 mm.

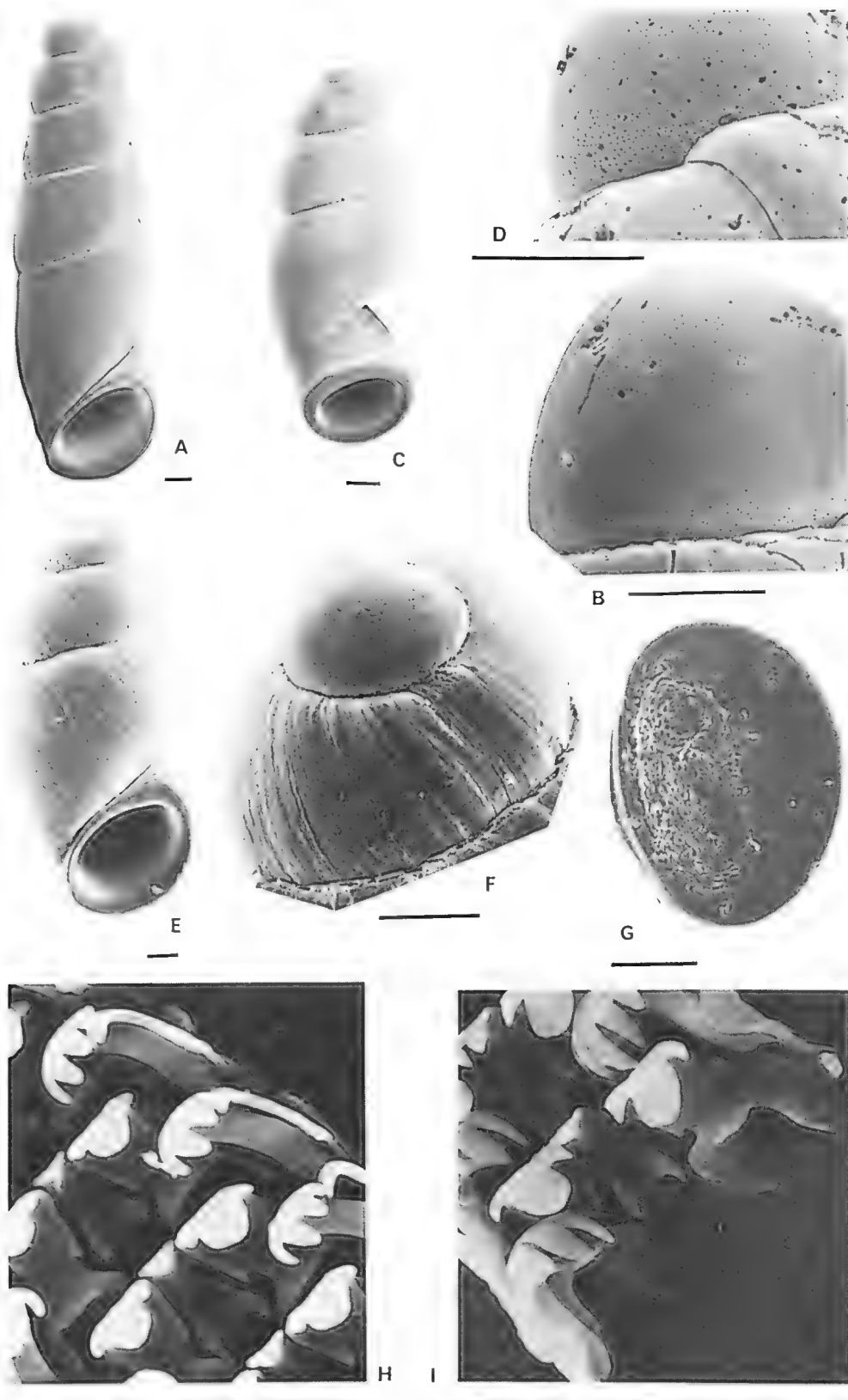


Fig. 23. A & B, *Badepigrus badius* (Petterd), type species of *Badepigrus* Iredale: A, shell; B, protoconch (Sow and Pigs Reef, Sydney, NSW, AMS C.137459). C & D, *Badepigrus protractus* (Hedley), type species of *Laseronula* Whitley: C, shell; D, protoconch (C, Shoal Point, Mackay, Queensland, AMS C.137461; D, Chinaman's Beach, Sydney, AMS C.137460). E–I, *Badepigrus pupoides* (Adams): E, shell; F, protoconch; G, operculum (inner side); H & I, radula (Simpsons Bay, Port Hacking, NSW, AMS C.137462). Scales: shells, protoconchs and operculum—0.1 mm; radulae—0.01 mm.

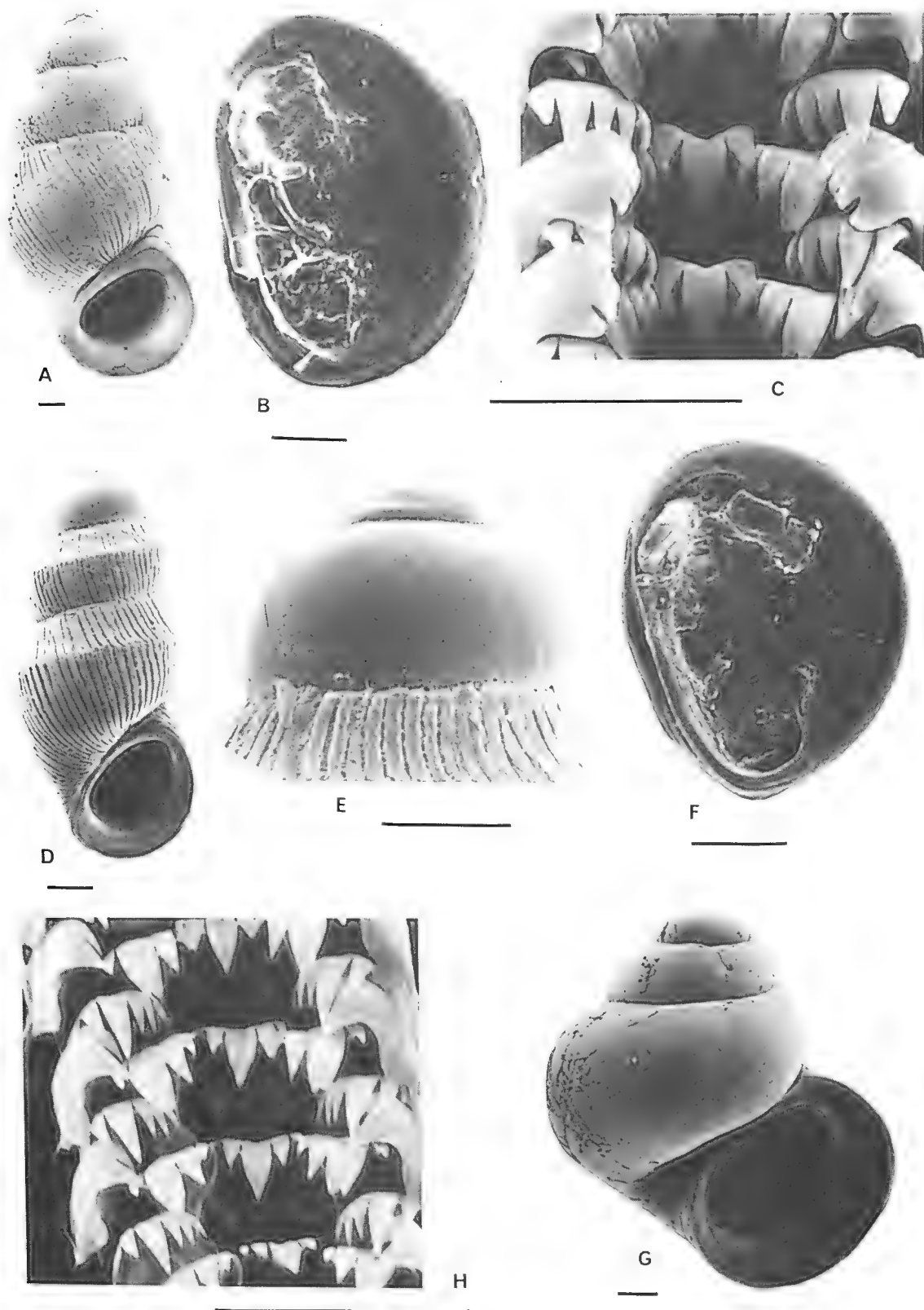


Fig. 24. A–C, *Afriscrobs africanus* (Bartsch), type species of *Afriscrobs* n.gen.: A, shell; B, operculum (inner side); C, radula (Agulhas, South Africa, AMS C.137463). D & E, *Afriscrobs eucosmius* (Turton) (? = form of *A. africanus*): D, shell; E, protoconch (Algoa Bay, Summerstrand, South Africa, NM B285). F–H, *Afriscrobs quantillus* (Turton): F, operculum (inner side); G, shell; H, radula (Millers Point, False Bay, South Africa, AMS C.107190). Scales: shells, protoconch and opercula—0.1 mm; radulae—0.01 mm.

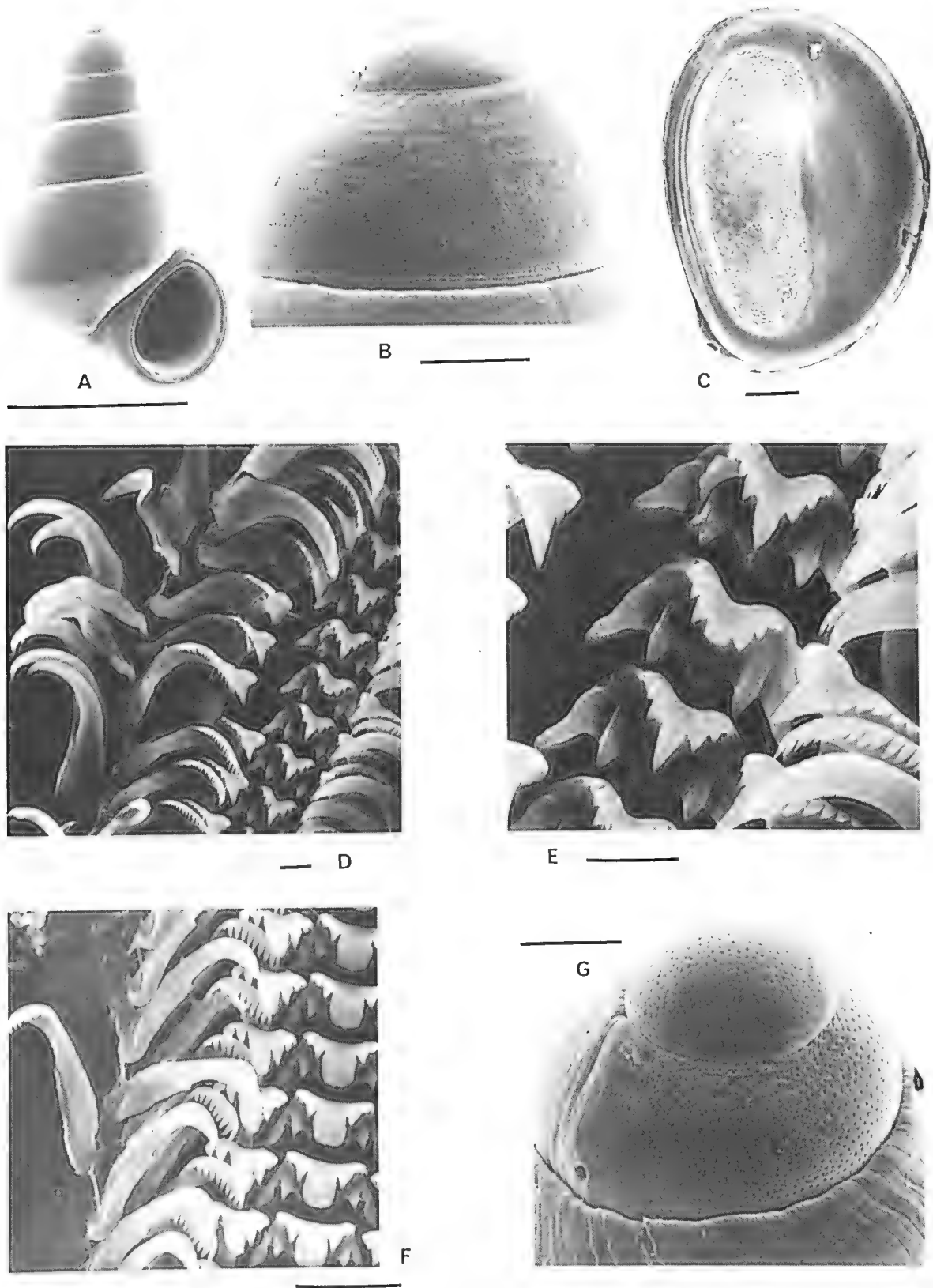


Fig. 25. A–E, *Pseudestea pyramidata* (Hedley), type species of *Pseudestea* Ponder: A, shell; B, protoconch; C, operculum (inner side); D & E, radula (E, detail of central teeth) (A & B, off Laurieton, NSW, 73 m, AMS C.137464; C, off Cronulla, NSW, 100 m, AMS C. 137475; D & E, off Watamooli, Sydney, NSW, AMS C.16308). F & G, *Pisinna punctulum* (Philippi), type species of *Pisinna* Monterosato and *Hagenmulleria* Bourguignat; F, radula; G, protoconch (Cala Rossa, Terrasini, Sicily, AMS C.137465). Scales; shell—1 mm; protoconchs and operculum—0.1 mm; radulae—0.01 mm.

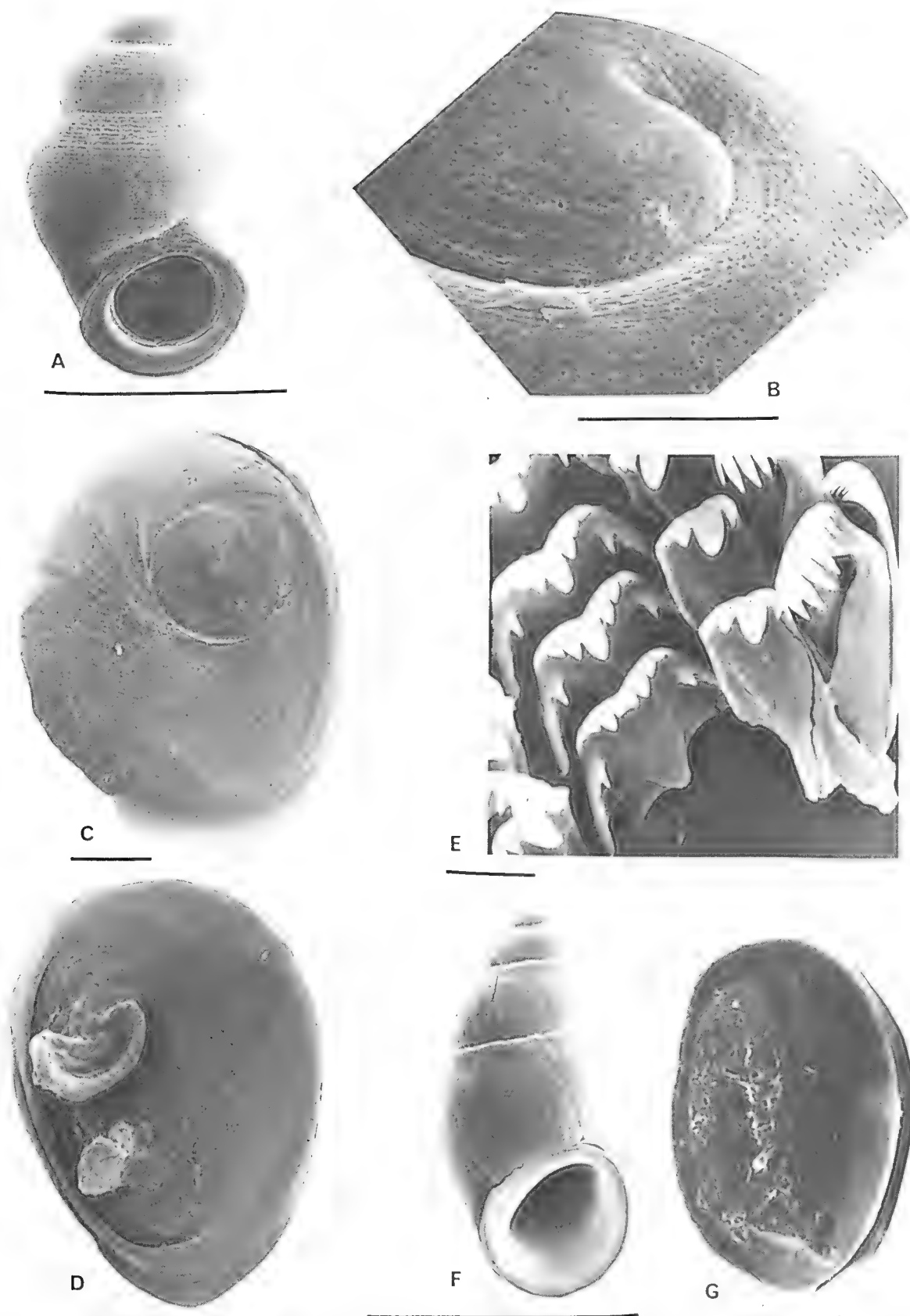


Fig. 26. A-E, *Nodulus contortus* (Jeffreys), type species of *Nodulus* Monterosato: A, shell; B, portion of protoconch showing microsculpture; C & D, operculum (C, outer side, D, inner side); E, radula (A, Palermo, Sicily, AMS C.137466; B-E, Posillipo, Naples, Italy, AMS, ex S. Palazzi). F & G, *Pisinna punctulum* (Philippi), type species of *Pisinna* Monterosato and *Hagenmulleria* Bourguignat: F, shell; G, operculum (inner side) (Cala Rossa, Terrasini, Sicily, AMS C.137465).

Scales: shells—1 mm; protoconch and opercula—0.1 mm; radula—0.01 mm.

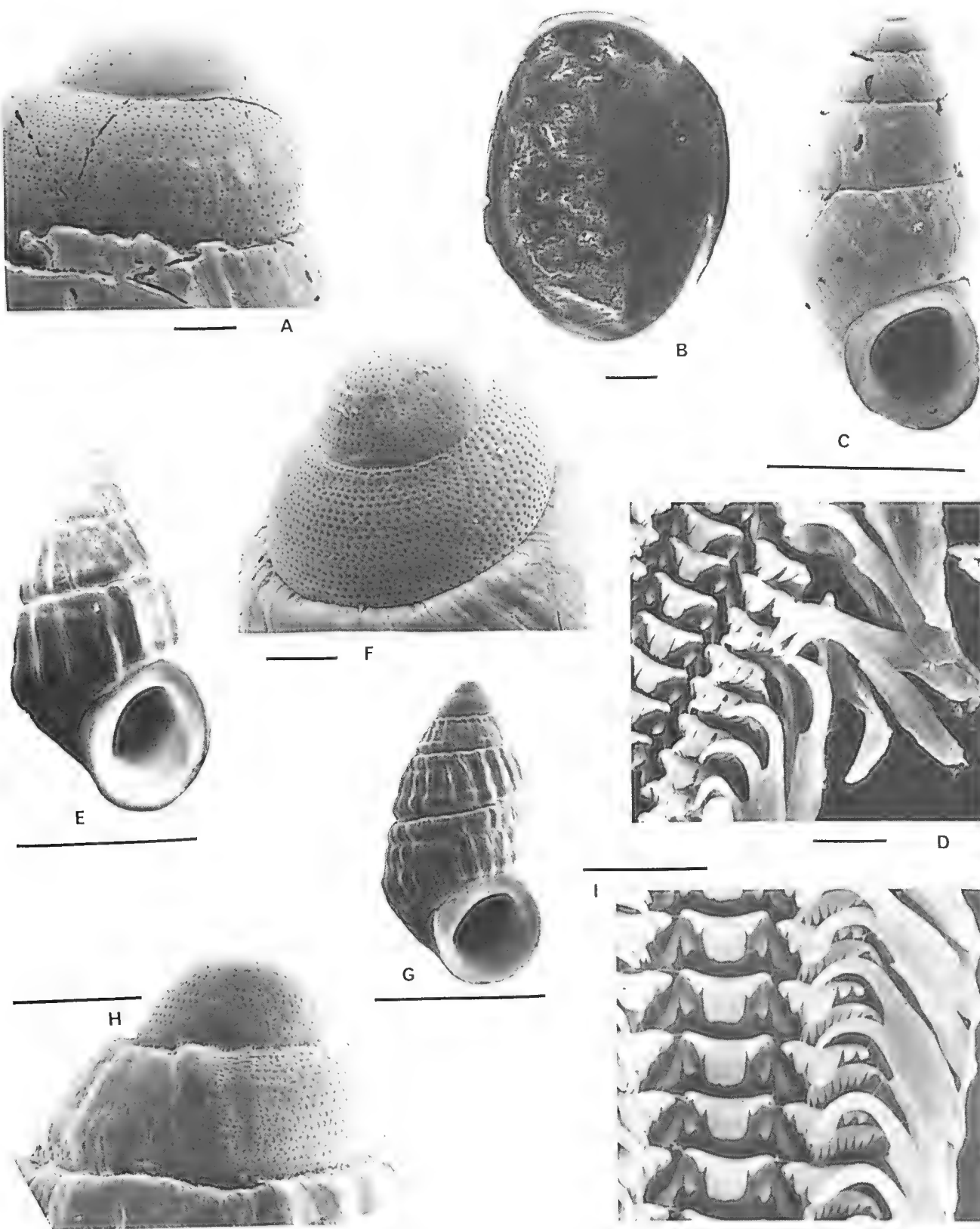


Fig. 27. A–D, *Pisinna zosterophila* (Webster), type species of *Estea* Iredale: A protoconch; B, operculum (inner side); C, shell; D, radula (probable paratypes, Devonport, Auckland, New Zealand, AMS C.17534). E & F, *Pisinna salebrosa* (Frauenfeld), type species of *Feldestea* Laseron: E, shell; F, protoconch (Bottle and Glass Rocks, Sydney, NSW, AMS C.137467). G–I, *Pisinna castella* (Laseron), type species of *Nodulestea* Iredale: G, shell; H, protoconch; I, radula (Ulladulla, NSW, AMS C.137468).

Scales; shells—1 mm; protoconchs and operculum—0.1 mm; radulae—0.01 mm.

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